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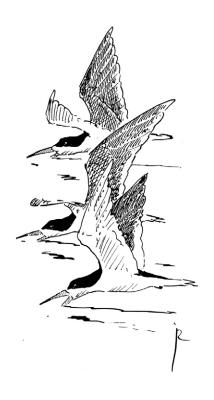
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Sexual dimorphism and diet segregation in the Black Skimmer *Rynchops niger*

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Sexual segregation during foraging is common in birds and may occur at different temporal and spatial scales. In this study we explored the degree of sexual segregation in the Black Skimmer Rynchops niger by studying the species and sizes of prey consumed by either sex. Moreover we assessed the distribution of the sexes over the study area. We developed a multivariate tool for sex determination in Black Skimmers by using morphometric measurements from birds of known sex. Birds captured with mist nets and museum skins were analysed. The sex of birds was determined by PCR amplification of DNA or by gonad inspection. The fish prey remains obtained from spontaneous regurgitations of captured birds were used to estimate total length and weight of consumed fish prey. The bulk of the diet of both sexes was generally composed of the same species (mostly silversides Odontesthes spp.), but males consumed larger prey than females. The sex ratio in the lagoon was strongly skewed towards females. We discuss the implications of sexual segregation for habitat and species conservation measures.

Key words: intraspecific diet segregation, sexual size dimorphism, wintering grounds, Black Skimmer, Rynchops niger

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INTRODUCTION

Several seabird studies reported differences in diet and feeding behaviour between males and females (González-Solís *et al.* 2000, Casaux *et al.* 2001, Barlow & Croxall 2002, Phillips *et al.* 2004). Sexual segregation is a relatively common characteristic in birds, and occurs at different temporal and spatial scales. It is generally considered to result from social dominance, competitive exclu-

sion, or niche specialization arising from differences in morphology or role during reproduction (González-Solís *et al.* 2000, Phillips *et al.* 2004). Sexual size dimorphism is a broad field of study which is subject to frequent debate because of difficulties in separating effects of different selection forces and identifying their interactions (Croxall 1995, Shine & Fairbairn 1995, Catry *et al.* 2005). In most species sexual differences are to some extent genetic and may also have an environmen-

tal component, so, different foraging specialization is likely to result as a consequence of sexual size dimorphism (Blackenhorn 2005). However, the relationship between sexual dimorphism and intersexual differences in foraging behaviour is not so clear, as patterns in behaviour observed in dimorphic species have been also observed in monomorphic species (Lewis *et al.* 2002).

Two broad categories of hypotheses formulated in regards to the selective forces raising and maintaining sexual size dimorphism can be distinguished: sex-related and environmental-related theories. The latter includes the 'intersexual competition hypothesis' or 'niche variation hypothesis' which states that sexual size differences reduce intra-pair and inter-sexual food competition, decreasing diet overlap, separating their feeding niches and exploiting a broader range of prey (González-Solís *et al.* 2000, Shaffer *et al.* 2001, Forero *et al.* 2002, Blackenhorn 2005).

The Black Skimmer Rynchops niger, as many other seabird species, has a monomorphic plumage but the sexes differ in several morphological traits (Ouinn 1990, Gochfeld & Burger 1994, Zusi 1996). The ability of making an accurate differentiation between sexes using non-destructive or non-invasive methods is essential in studies of long-lived birds. Although there is some information about the feeding ecology and sexual size dimorphism for several North American breeding populations of Black Skimmer (Quinn 1990), there is a complete lack of information for South American populations throughout the year. During the breeding season, Black Skimmers establish small colonies next to rivers (Klimaitis Moschione 1984, Canevari et al. 1991); during the non-breeding season the birds congregate in large numbers near estuarine and coastal areas. Recently, in Argentina, several studies addressing the feeding ecology and diet of Black Skimmers were conducted (Favero et al. 2001, Mariano-Jelicich et al. 2003, Silva Rodríguez et al. 2005, Mariano-Jelicich & Favero 2006), but sex differentiation or dietary and/or behavioural differences among sexes have not been studied. The aim of this study is to (1) analyse sexual size dimorphism to develop a multivariate tool for determining the sex in South American Skimmers, and (2) analyse the degree of intraspecific segregation in diet and distribution.

METHODS

Study Area

The study was conducted between October 2003 and May 2005 at Mar Chiquita coastal lagoon (37°40'S, 57°22'W), Buenos Aires Province, Argentina (MAB-UNESCO Reserve; Fig. 1). During the austral summer and autumn between 5000 and 10 000 Black Skimmers roost in Mar Chiquita, which is the most important documented wintering area for the species in southern South America.

Sampling

Morphometrics of 78 birds were used, 55 of them were caught with mist nets (9 males and 46 females), and the remaining 23 (9 males and 14 females) were museum skins from the Museo de Ciencias Naturales de La Plata (La Plata, Argentina) and the Museo de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina). The museum birds had been collected during the non-breeding season in other coastal locations at Buenos Aires Province. Four morphological measurements were taken: culmen length (distal point of the bill up to the notch at the base of the bill), lower bill length, tarsus-metatarsus length (for these three measures digital callipers \pm 0.01 mm were used) and the maximum (flattened) wing length (wrist joint to the tip of the longest primary, measured to the nearest millimetre with a stopped metric ruler). As morphometric measurements of museum skins and captured birds were not statistically different (Mann-Whitney test, P > 0.05) samples were pooled. Body mass of captured birds was measured to the nearest 5 g. As all individuals were adults captured during the non-breeding season, we were confident that their body mass was not biased due to different reproductive status. Blood samples (between 200 and $500 \,\mu l$) were taken from the brachial vein with a syringe, collected in

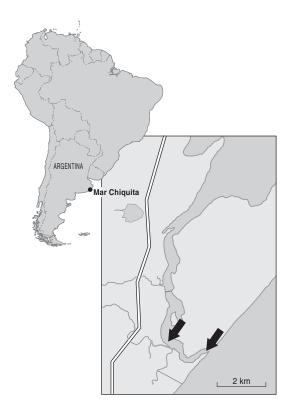


Figure 1. Location of Mar Chiquita Coastal Lagoon (37°40'S, 57°22'W), Buenos Aires Province, Argentina, with a detail of the study area at Mar Chiquita Coastal Lagoon. Arrows indicate main concentrations of Black Skimmers.

a tube containing 1.5 ml absolute ethanol and stored at room temperature until analysis.

Individuals were sexed by two methods: (a) gonad inspection in museum specimens, and (b) polymerase chain reaction (PCR) amplification of DNA with blood samples taken from individuals captured with mist-nets. The primers used for the PCR amplification were 2550F and 2718R (manufactured by INVITROGEN Life technologies) (see Fridolfsson & Ellegren 1999). The PCR thermal profile was followed from Fridolfsson & Ellegren (1999). PCR products were separated in 1.2% agarose gels, run in standard 1x TBE buffer and visualized by ethidium bromide staining. PCR

products were compared to 100 bp DNA ladder. Males were recognized as displaying a single PCR product (from CHD1Z, 600 bp) while females showed two PCR products (from CHD1W, 450 bp – and from CHD1Z) (Fridolfsson & Ellegren 1999).

Dimorphism between males and females was calculated for each variable using the Storer's index (SI)

 $SI = (V_m - V_f) / [(V_m + V_f) \times 0.5]$ where V_m corresponds to the mean value for males and V_f to the mean value for females of the variable considered (Storer 1966, Blondel *et al.* 2002, González-Solís 2004).

Sex ratio observations

Taking advantage of the remarkable difference in bill size between sexes, sex ratios were determined by direct counts on digital photographs taken at the main roosting sites of Black Skimmers in the study area. A total of 18 pictures, taken during mid-summer when large numbers of Skimmers are seen at Mar Chiquita Coastal Lagoon were analysed using ImageJ software (Rasband, W.S., ImageJ, US National Institutes of Health, Bethesda, Maryland, USA, 1997–2006). Only birds that could be unequivocally sexed from the pictures were included in the analysis.

Diet analysis

Spontaneous regurgitations were collected monthly from birds captured in mist nets between October and May 2003–2004 and 2004–2005. Each sample was kept in 70% ethanol until analysed. Prey were identified to the lowest possible taxonomic level using keys, illustrations and descriptions from literature (Cousseau & Perrota 1998) and reference material from our collection.

Total length (TL) and mass (M) of fish prey were determined by two different methods: (1) in case of undigested prey by measuring TL with a digital calliper (0.01 mm) and M with an electronic balance (0.01 g), and (2) in partially digested prey by estimating both TL and M as described in Mariano-Jelicich & Favero 2006. The weight of each regurgitated sample was calculated from the weights of separate prey remains.

The relative importance of prey categories was quantified as: (1) frequency of occurrence (F%), which is the percentage of samples that contained a particular prey category, (2) numerical abundance (N%) as the percentage of prey items of a particular type out of all prey items, and (3) the percentage of biomass (M%) provided by a particular prey item out of the estimated total biomass consumed (Duffy & Jackson 1986, Rosenberg & Cooper 1990). Those parameters were combined into an Index of Relative Importance (IRI) and IRI% for each prey category (i), (Sanger 1987, Silva Rodríguez *et al.* 2005) as:

$$IRI_i = F_i\% (N_i\% + M_i\%),$$

 $IRI_i\% = (IRI_i \times 100) / IRI_{total}$

Statistics

Morphological differences between sexes were assessed by Mann-Whitney tests (Zar 1999). In

order to obtain discriminant functions, sexed individuals were subjected to Discriminant Function Analyses (Statistica 6). For these analyses 30 randomly selected females and the complete set of males were used. The analyses were applied even though some of the variables were not normally distributed, as there is evidence that this violation does not inflate the significance of the tests (Hair *et al.* 1995). Sample sizes for the different combination of variables varied as not all measurements were taken from each individual.

For the comparison of regurgitation masses between sexes, a random sub-sample of 24 female regurgitations and the complete set of male regurgitations were used to equal the sample sizes for each sex. A Student's t-test was applied in order to assess differences between sexes. Differences between sexes of IRI% of fish prey were compared with χ^2 goodness-of-fit test (the categories *Anchoa*

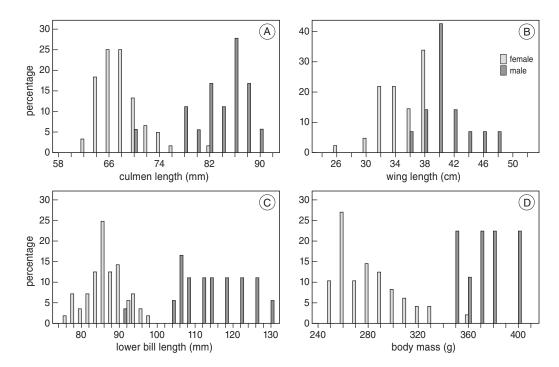


Figure 2. Frequency distributions of morphometric measurements and body mass in male and female Black Skimmers. Given are (A) culmen length (male n = 18, female n = 60), (B) wing length (n = 14 and 41), (C) lower bill length (n = 18 and 58), (D) body mass (n = 9 and 48).

marinii, Lycengraulis grossidens and 'unidentified fish' were combined for the analysis). Mann-Whitney *U*-tests were used to compare the sizes of fish prey by sex. A Kolmogorov-Smirnov *D*-test was used to compare the frequency distributions of fish prey sizes.

RESULTS

Morphometric differences between sexes

Black Skimmers were sexually dimorphic for all the parameters measured, males being larger than females (Fig. 2). The Storer's index of body mass was 28% higher in males than in females. Large differences were also found in culmen length (Δ SI 38%) and lower bill length (Δ SI 27%), while the dimorphism was smaller for tarsus and wing length (Δ SI 13% and 16%, respectively). Uni-

variate comparisons of the different parameters were all significantly different between males and females (Table 1). However, given the overlap on the tails of the distributions of almost all the parameters, it was useful to determine other functions to allow an accurate differentiation between females and males. Discriminant function analysis showed that lower bill length, body mass and culmen length correctly assigned the sex of Skimmers over 90% of the cases (97.9%, 97.2% and 93.7%, respectively), and wing length and tarsus length in 87.9% and 83.3% of the cases, respectively. From all discriminant functions constructed with combinations of these parameters, the model including culmen length and lower bill length was considered the most convenient function given its high discriminant power (correctly classifying 97.9% of the birds) and its practical application due to the few variables required (Table 2).

Table 1. Morphometric measurements for the overall sample and for each sex of Black Skimmer in Mar Chiquita Coastal Lagoon, Buenos Aires Province, Argentina. Data are presented as mean \pm 1 SD and sample size between brackets.

Parameter	Total	Males	Females	M-W ^a	P
Culmen length (mm)	68.4 ±7.8 (78)	80.5 ±5.1 (18)	64.8 ±3.7 (60)	6.2	< 0.001
Lower bill length (mm)	$92.2 \pm 13.2 (74)$	112.5 ±9.9 (18)	$85.7 \pm 4.9 (56)$	6.3	< 0.001
Tarsus length (mm)	$30.8 \pm 2.6 (78)$	$33.9 \pm 2.2 (18)$	$29.8 \pm 2.0 (60)$	5.1	< 0.001
Wing length (cm)	$35.4 \pm 4.0 (55)$	40.0 ±3.3 (14)	$33.9 \pm 2.9 (41)$	4.9	< 0.001
Body mass (g)	292.1 ±41.3 (57)	369.4 ±19.3 (9)	277.6 ±24.6 (48)	4.7	< 0.001

^aMann-Whitney *U* test.

Table 2. Discriminant functions obtained through discriminant function analyses for the Black Skimmer in Mar Chiquita Coastal Lagoon, Buenos Aires Province, Argentina.

Discriminant function ^a		F(df)	T%c	F% ^d	M%e
$=0.138 \times LBL + 0.26 \times WL + 0.166 \times CL + 0.014 \times W + 0.26 \times TML - 45.31$ $=24.04 - 0.123 \times CL - 0.115 \times LBL - 0.0001 \times TML - 0.02 \times W$ $=16.15 - 0.098 \times LBL - 0.09 \times CL$	0.04	73 (5,15) <i>P</i> < 0.001	100	100	100
	0.11	64.7 (4,31) <i>P</i> < 0.001	100	100	100
	0.20	90.0 (2,45) <i>P</i> < 0.001	97.9	100	94.4

^aLBL= lower bill length; WL= wing length; CL= culmen length; TML= tarsus-metatarsus length; W= body mass.

^bWilks-lambda (from 0 to 1 for maximum and minimum discriminant power).

^cPercentage correctly classified individuals.

^dPercentage correctly classified females.

ePercentage correctly classified males.

Sex ratio

Taking into account the strong dimorphism in the bill structure, 530 individuals were counted on 18 pictures of Skimmer flocks. The average sex ratio calculated for the area was strongly skewed towards females with 4.9 female: 1 male.

Diet segregation

A total of 50 spontaneous regurgitations were obtained, 42 of them belonged to females and eight to males. A total of 481 fish prey were identified from the samples. Male regurgitations contained only fish items (100%) while crustaceans were found in two female samples.

Five fish species were identified from the regurgitated samples: 'Pejerrey' Silverside Odontesthes argentinensis, 'Cornalito' Silverside O. incisa, Brazilian Menhaden Brevoortia aurea, Atlantic Sabretooth Anchovy Lycengraulis grossidens and Anchovy Anchoa marinii (Table 3). The Atlantic Sabretooth Anchovy was never found in male regurgitations. Differences between sexes were observed when comparing the IRI% of the different fish prey $(\chi^2_4 = 2026, P < 0.001)$, which is mainly determined by the higher IRI% values of O. argentinensis in males compared to females. For both sexes, the most important prey were the two silverside species 'Cornalito' and 'Pejerrey' (together accounting for 70% and 77% of the diet of males and females, respectively), followed by Menhaden.

Weights of regurgitations were not statistically different between males and females (39.0 \pm 24.5 g, n = 8 and 29.6 \pm 19.4 g, n = 24, respectively; $t_{30} = 1$, P = 0.30).

The median size of fishes caught did not vary significantly between the sexes (male prey were 0.4% larger and 8.8% heavier than those of females; M-W $Z_{390, 91} = 0.54$, P = 0.59 for TL and M-W $Z_{390-91} = 1.24$, P = 0.20 for M; Fig. 3A and B). However, the frequency distributions of fish prey length differed significantly between the sexes (K-S D = 0.19, P < 0.001). When the analysis was restricted to the silverside species O. argentinensis, significant differences both in total length and weight were observed (male prey were 21.5 % larger and 49.4 % heavier than prey of females, median TL for males: 81.7 mm vs. 63.7 mm for females; and median M for males: 3.75 g vs. 1.7 g for females; M-W $Z_{72, 15} = 3.87$, P = 0.0001; K-S D = 0.0 P < 0.001 for TL, and M-W $Z_{72, 15} = 3.8$, P = 0.0001; D = 0.025, P < 0.001 for M) (Fig. 3C) and D). However no significant difference was found for the silverside species O. incisa (female prey were 2.4% larger and 6.7% heavier than male prey; median TL for males: 77.6 mm vs. 82.2 mm for females and median M for males 2.5 g vs. 2.8 g for females; M-W $Z_{229, 49} = 0.93$, P = 0.30, K-S D = 0.21, P > 0.05 for TL, and M-W $Z_{229, 49} =$ 0.51, P = 0.60, K-SD = 0.2, P > 0.1 for M.

Table 3. Fish prey of Black Skimmer males and females at Mar Chiquita, based on regurgitations. Data are presented by importance of number (N%), frequency of occurrence (F%), importance by mass (M%) and index of relative importance (IRI%).

	Males			Females				
	N%	F%	М%	IRI%	N%	F%	М%	IRI%
Anchoa marinii	2.2	12.5	1.8	0.4	1.0	4.8	0.9	0.1
Brevoortia aurea	11.0	12.5	13.7	2.6	3.1	19.0	5.7	1.2
Lycengraulis grossidens					0.3	2.4	0.5	0.01
Odontesthes argentinensis	16.5	62.5	24.7	21.7	18.5	28.6	15.7	6.7
Odontesthes incisa	53.8	87.5	43.5	71.8	58.7	97.6	56.9	77.2
Atherinidae	16.5	12.5	16.3	3.5	17.9	57.1	20.1	4.9
Unidentified fish					0.5	2.4	0.2	0.01

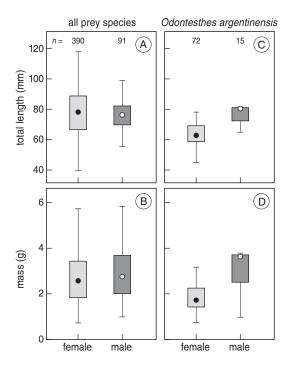


Figure 3. Comparison of (A) total length and (B) mass of all consumed prey species taken by male and female Black Skimmer. Separately given are (C) total length and (D) mass of silversides *Odontesthes argentinensis*. Indicated are median, 25–75% quartiles (boxes), range without outliers (whiskers), and sample sizes.

DISCUSSION

The Black Skimmer is a sexually dimorphic seabird, with males being larger than females, as described in the literature (Erwin 1977, Burger & Gochfeld 1992, Gochfeld & Burger 1994, Quinn 1990, Zusi 1996). The mean values of some measurements in this study were in line with those from North America (see Burger & Gochfeld 1992, Quinn 1990), but methodological incompatibilities preclude detailed comparisons.

Considering that the tails of the frequency distributions for separate morphometric parameters overlapped, the construction of a discriminant function is of great value to classify birds by sex. In this paper we provide a simple and accurate func-

tion with few variables that discriminates among sexes. A discriminant function for a North American breeding population of Black Skimmers was constructed by Quinn (1990), but as birds may have a strong breeding site fidelity, discriminant functions developed for one breeding population are unlikely to work in another (Genovart et al. 2003, Mallory & Forbes 2005). We suggest that the population wintering at Mar Chiquita Coastal lagoon consists of birds from various breeding populations given the high densities observed (c. 10 000 adult individuals) compared to those occurring in breeding areas of southern South America (i.e. colonies are smaller than one hundred pairs; Klimaitis & Moschione 1984, Canevari et al. 1991, Raffo pers. comm.). However, we do not know to what extent Black Skimmers from different breeding locations are spatially segregated at Mar Chiquita. If they segregate, then the captured birds may not represent a mixed assortment of birds from multiple breeding populations. So, further studies on the distribution of Skimmers at Mar Chiquita are needed before the discriminant function given here can be applied to other Skimmer populations.

The female diet, including different taxonomic prey such as crustaceans, appears to be more diverse than the male diet. This conclusion should be considered preliminary given the small sample sizes of males. However, we can conclude that the diet of both sexes was dominated by fish, which is in line with the extant information on the species. The most important fish prey species for both sexes were the silversides Odontesthes incisa and O. argentinensis, followed by Menhaden B. aurea. The presence of silversides corroborated with previous studies from the same study area when pellets were analysed (Mariano-Jelicich et al. 2003). On the other hand, the presence of B. aurea in the regurgitations contrasted with information from previous studies, where this fish was only occasionally found in the diet (Favero et al. 2001, Mariano-Jelicich et al. 2003, Silva Rodríguez et al. 2005, Mariano-Jelicich & Favero 2006). The feeding tactic used by Skimmers, inserting the lower mandible in the water, thus exploring the upper 10 cm of the water column prevents them to forage on pelagic fish. They only capture benthic prey from very shallow waters. This particular feeding tactic could explain the relatively moderate differences found in the prey species between the sexes and the lower diversity of the Skimmer diet compared to the diet of other larids in the study area (Mauco & Favero 2004, Silva Rodríguez *et al.* 2005). On the other hand, sexual differences in the relative consumption of certain fish prey were observed, with a higher occurrence of Menhaden in the female diet and higher occurrence of *Odontesthes argentinensis* in the diet of male Skimmers.

Even thought no sex differences were observed in terms of the overall prey sizes, the size-frequency distributions did differ, which showed that males took larger prey than females. This trend was also observed when only *Odontesthes argentinensis* was considered. The lack of differences in *Odontesthes incisa* sizes between males and females could be attributed to the fact that the maximum length captured by female Skimmers (151.7 mm) corresponded to the maximum length described for this fish species (about 150 mm, Cousseau & Perrota 1998).

At Mar Chiquita Coastal Lagoon, three main areas can be identified considering water salinity. Odontesthes argentinensis distribute differently along these areas, with larger sizes found to the north closer to the tributaries of the lagoon, while medium and smaller sizes are mostly distributed among the estuarine areas (southern tip of the lagoon) (Cousseau et al. 2001). The observed differences in the consumption of Odontesthes argentinensis sizes between male and female Skimmers might be attributed to the use of different foraging areas, and warrants further exploration. A differential use of foraging areas between sexes has also been suggested from recent studies using radiotelemetry devices and analysis of stable isotopes (Mariano-Jelicich, unpubl. data).

As emphasized before, we encountered difficulties to catch sufficient males. Obviously this could be partially explained by the sex ratio in the study area, being strongly skewed toward the females. There are many examples in the literature of birds showing differences between sexes on the distribution to, use of and/or preferences for certain wintering areas (Robertson & Cooke 1999, Croxall *et al.* 2005, Phillips *et al.* 2005).

Most of the studies comparing sexual size dimorphism and differences in foraging behaviour are limited to the reproductive season (including Skimmers, Quinn 1990), while studies undertaken during the non-breeding season are rare. Gathering information on seabirds' ecology during the nonbreeding season is particularly important considering that it is an important period to ensure individual survival and future reproductive success (Sherry & Holmes 1995, Favero & Becker 2006). Skimmers (along with other seabird species) make an intensive use of coastal and estuarine areas as wintering sites throughout its distribution range. depending on resources often affected by human activities like sport fishing and tourism (Copello & Favero 2001, Mauco & Favero 2004, Silva Rodríguez et al. 2005). These considerations show the necessity of studies on species ecology, particularly those accounting for sex differences as a valuable tool for the elaboration and implementation of conservation and management plans at the wintering areas.

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SAMENVATTING

Het gescheiden voorkomen van de geslachten in tijd en ruimte is een algemeen verschijnsel bij vogels. Dit hangt vaak samen met sekseafhankelijke verschillen in foerageergedrag en voedselkeuze. De ontwikkeling van voorkeuren kan hebben bijgedragen aan of een gevolg zijn van de evolutie van seksuele dimorfie. In het hier gepresenteerde onderzoek wordt onderzocht of bij overwinterende Amerikaanse Schaarbekken Rynchops niger een dergelijke sekseafhankelijke voedselvoorkeur aanwezig is. De studie werd uitgevoerd in Mar Chiquita, een lagune aan de kust van Argentinië (Buenos Aires Provincie: 37°40'ZB, 57°22'WL). In dit MAB-UNESCO Reservaat overwinteren elk jaar 5,000-10,000 schaarbekken. Mannetjes schaarbekken hebben een opmerkelijk grotere snavel dan vrouwtjes. Schattingen aan de hand van fotobeelden wijzen erop dat de geslachtsverhouding in de lagune erg scheef ligt. Er overwinteren vijfmaal zoveel vrouwtjes als mannetjes. De auteurs ontwikkelden een discriminantfunctie om de seksen nauwkeurig op basis van een combinatie van morfologische kenmerken te kunnen onderscheiden. Omdat schaarbekken lastig te vangen bleken, werden gegevens verkregen uit mistnetvangsten aangevuld met gegevens van museumbalgen. De discriminantfunctie werd getest voor individuen met een bekend geslacht en bleek in 97,9% van de gevallen het juiste geslacht toe te wijzen. Het geslacht van de gebruikte individuen was bepaald aan de hand van bloedmonsters en moleculaire PCR-technieken of door onderzoek van de gonaden. Vervolgens werd voor elk geslacht de voedselvoorkeur en de lichaamslengte en het gewicht van de gegeten prooien bepaald aan de hand van de braaksels, die gevangen vogels vaak 'spontaan' produceren. Beide geslachten bleken vooral 'silversides' te eten (Odontesthes argentinensis en O. incisa), een algemene visje in neotropische lagunes. Mannetjes aten meer O. argentinensis (de grootste van de twee 'silversides') dan vrouwtjes. Mannetjes aten ook significant grotere O. argentinensis: tot 4 cm langere en 50% zwaardere vissen dan vrouwtjes. Schaarbekken pikken hun prooien van vlak onder het wateroppervlak op. Daarbij wordt alleen de ondersnavel in het water gestoken. De auteurs nemen aan dat mannetjes met hun iets grotere snavel beter in staat zijn grotere vissen op te scheppen en daarom andere delen van de lagunes gebruiken dan de vrouwtjes. De sekseafhankelijke verschillen in geconsumeerde prooigroottes zou ook de scheve geslachtsverhouding in de lagune kunnen verklaren. (YIV)

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