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## TEMPORAL VARIATION IN THE FEEDING ECOLOGY OF THE BLACK-FACED IBIS (*THERISTICUS MELANOPIS*) IN PASTURES OF SOUTHERN CHILE

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**Resumen.** – Variación temporal de la ecología alimentaria de la Bandurria (*Theristicus melanopis*) en praderas agrícolas del sur de Chile. – Las variaciones temporales en la disponibilidad de alimento pueden generar cambios en las estrategias alimentarias y preferencias tróficas de los animales. Entre Mayo 1999 y Enero 2000 evaluamos la variación temporal del comportamiento alimentario, la composición de la dieta y la disponibilidad de presas para la Bandurria (*Theristicus melanopis*) en praderas agrícolas del sur de Chile. Las muestras de suelo mostraron que los invertebrados hipógeos tales como las lombrices de tierra (*Lumbricus* spp.), el Gusano cortador (*Agrotis* spp.), la Cuncunilla negra (*Dalaca* spp.) y el Pololo verde (*Hylamorpha elegans*) fueron las presas más abundantes en las praderas y sus poblaciones experimentaron marcadas variaciones durante el período de estudio. Las larvas de insectos fueron los principales constituyentes de la dieta de la Bandurria y fueron consumidas en mayor proporción que lo esperado por azar. La composición de la dieta (basada en análisis fecales) y las preferencias tróficas coincidieron con la variación en la disponibilidad de estas presas. Durante períodos con una reducida abundancia de presas, las bandurrias consumieron mayor número de presas diferentes y se redujo la tasa de consumo. Al mismo tiempo, la abundancia de bandurrias disminuyó en el área de estudio. Estas variaciones fueron más evidentes a fines de la primavera y el verano, cuando la abundancia de presas en las praderas es menor que en las otras estaciones. Nuestros resultados sugieren que los ciclos de vida de las presas constituyen el principal factor causal que influye en la ecología trófica de la Bandurria en praderas agrícolas del sur de Chile.

**Abstract.** – Temporal variation in food availability may generate changes in the feeding strategies and trophic preferences of animals. We studied the temporal variation in feeding behavior, diet composition, and prey availability of the Black-faced Ibis (*Theristicus melanopis*) in pastures of southern Chile between May 1999 and January 2000. Soil core samples showed that hypogeous invertebrates such as, earthworms (*Lumbricus* spp.), black cutworm larvae (*Agrotis* spp.), black pasture caterpillars (*Dalaca* spp.), and southern green chafers (*Hylamorpha elegans*) were the most abundant prey in the pastures and that their populations experienced pronounced seasonal variations. Insect larvae were the main prey of the Black-faced Ibis and were consumed in greater proportion than expected by chance. The diet composition (based on feces) and trophic preferences coincided with variations in prey availability. During periods of reduced prey abundance Black-faced Ibises foraged on more different types of prey and their consumption rate diminished. At the same time, the abundance of Black-faced Ibises decreased in the study area. These variations were most evident in late spring and summer, when prey abundance in the pastures was lower than in the other seasons. Our results suggest that the life cycle of the prey is the

main causal factor that influences the feeding ecology of the Black-faced Ibis in pastures of southern Chile.

**Key words:** Agro-ecosystems, Black-faced Ibis, Chile, diet, prey availability, seasonality, *Theristicus melanopis*, Threskiornithidae.

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## INTRODUCTION

Temporal variation in food availability can influence population dynamics, reproductive success and generate changes in foraging strategies (Martin 1987, Chamberlain *et al.* 1999, Gawlik 2002, Ardia *et al.* 2006, Ramos 2011). Numerous species of birds live in habitats with significant fluctuations in food availability during the annual cycle and frequently encounter periods of shortage (Newton 2013). As a consequence, many birds must adopt more flexible feeding strategies in synchrony with variations in prey availability (Clergeau & Yésou 2006, Herring *et al.* 2010, Herring & Gawlik 2013). Birds can respond to shortages in resources, by increasing the search time (Kushlan 1981, Beerens *et al.* 2011), changing their foraging behavior (Lovette & Holmes 1995, Jahn *et al.* 2010, Beerens *et al.* 2011, Ghosh *et al.* 2011), trophic preferences (Morse 1990), and varying their diet composition (Naef-Daenzer *et al.* 2000). Foraging theory predicts that prey availability influences feeding strategies, increasing the trophic niche of species when food is scarce and reducing niche size when food is abundant (Krebs 1978, Todd *et al.* 1998, Beerens *et al.* 2011, Margalida *et al.* 2012).

Environmental conditions and prey life cycles are considered to be two important, easily identifiable factors that determine food availability for birds (Morse 1990). In tropical and subtropical wetlands, wading birds, such as many species of ibises (family Threskiornithidae), modify their feeding strategies according to prey availability which, in turn,

depends on the environmental conditions, especially during the dry season (Kushlan 1979, Safrán *et al.* 2000, Lorenz *et al.* 2009, Beerens *et al.* 2011, Herring & Gawlik 2013).

In the agroecosystems of southern Chile, earthworms and larvae of *Agrotis* spp. (Lepidoptera, Noctuidae), *Dalaca* spp. (Lepidoptera, Hepialidae), and *Hylamorpha elegans* (Coleoptera, Scarabaeidae) constitute the most important prey items in the diet of the Black-faced Ibis (*Theristicus melanopis*) (Gantz & Schlatter 1995, Gantz 2010). However, existing information on diet is restricted to the Austral winter, and the relationships between temporal variation in prey availability and ibis feeding ecology remain unexplored. Seasonal fluctuations in climatic conditions may change invertebrate assemblages available as food in the temperate agroecosystems of southern Chile. It is likely that the Black-faced Ibis responds to such changes by modifying its feeding strategies accordingly throughout the annual cycle. In this study, we assess whether diet composition and trophic preferences of the Black-faced Ibis correlate with variations in the availability and composition of invertebrate assemblages present in southern Chilean pastures.

## METHODS

*Study area.* We carried out this study in an area of 178 ha near Chahuilco (40°43'37"S, 72°51'13"W), province of Osorno, southern Chile over a period of 9 months, between May 1999 and January 2000. This area corresponds to pastures destined for intensive cat-

tle production, and is commonly used for foraging by Black-faced Ibises.

The vegetation is dominated by associations of annual grasses (Poaceae), with the presence of dispersed *Nothofagus dombeyi* (Nothofagaceae) and *Laurelia sempervirens* (Atherospermataceae) trees used by the Black-faced Ibis as nesting substrate. The climate in this region is warm-temperate, with monthly mean temperatures between of 10 and 12°C and mean annual precipitation ranging between 1200 and 1800 mm. The primary rainy season occurs between May and August (Subiabre & Rojas 1994, CONAMA 2008).

*Relative abundance of invertebrates.* We used 39–80 random soil-core samples to estimate the total relative monthly (May–January) abundance of invertebrates (potential prey) (Lee 1985) in order to establish temporal variation in invertebrate species availability in pastures where Black-faced Ibises were more abundant. Random samples were obtained by throwing a sharp pointed stick into the air with rotating movement, indicating orientation (Mac Arthur & MacArthur 1961). The distance to the sample collection location was measured according to number of steps obtained with a random number table. We obtained a soil volume of 19 x 19 cm width and 10 cm depth (Lee 1985) using a square shovel. Given that the mean beak length of the Black-faced Ibis is 130.37 mm (SE = 8.31, n = 28; data obtained from specimens collected in previous studies, Gantz unpub. data), all invertebrates present within this depth range were considered as potentially available and accessible prey for the birds. Soil samples in the field were thoroughly separated by hand prior to the analysis, and all invertebrates detected were counted. We weighed the invertebrates separately by type with an Ohaus portable balance (+/- 0.01 g) to quantify the biomass contributed by each invertebrate type.

*Diet.* We evaluated monthly variation in the diet of the Black-faced Ibis through fecal analysis. Although fecal analyses are subject to biases due to different prey digestibility (Rosemberg & Cooper 1990, Macías *et al.* 2004), this was the only ethically, economically, and logistically reasonable method to study diet on a monthly basis. Fresh fecal samples were collected in the field, stored in bags, and transported to the laboratory for analysis. Fecal samples were washed in a sieve (ca. 0.1 mm mesh aperture) and deposited in petri dishes to be examined under a stereoscopic microscope. We counted all the identifiable remains of elytra and jaws (left and right), and heads, then divided the number of elytra and jaws by two and quantified the heads (cephalic tagma) individually (Calver & Wooler 1982). Two elytra and two jaws of opposite sides, and one head were considered as one individual. When possible, we identified all prey at species level with the aid of entomological guides (González 1989, Etcheverry & Herrera 1971), reference collections, and the collaboration of experts at SAG (Livestock and Agriculture Service) Entomology Laboratory in Osorno, Chile.

*Foraging behavior.* We evaluated differences in the prey consumption rate to verify if consumption rate and relative prey abundance covaried. Foraging ibises were observed from a vehicle at distances of ca. 15–400 m, using a telescope (20–60 x 70). For each focal individual, selected as closest to the observer (Lehner 1996), consumption rate (20–70 monthly observations) and search time (66 observations in May, 90 in July, and 26 in December) were recorded. Observations were stopped when the focal individual moved out of sight of the observer, and when the bird flew away, e.g., as a result of any kind of disturbance. We defined consumption rate as the number of prey captured on or below the ground, per minute. Direct observation of the sharp, iner-

tial head movement, which precedes swallowing, indicated prey consumption. Immediately after determining the consumption rate, we quantified the prey-search time of Black-faced Ibis in the field (Lovette & Holmes 1995, Collazo *et al.* 2010). We considered search time as the time lapse between two successful captures measured with a digital chronometer.

*Environmental variables.* Given that precipitation can affect the availability of food resources and soil hardness (Jahn *et al.* 2010, Catry *et al.* 2012), we used monthly rain statistics (through the study period) gathered at Cañal Bajo Airport meteorological station (Osorno, Chile), located approximately 20 km away from the study area. Additionally, we obtained 20–60 measures of soil hardness ( $\text{kg}/\text{cm}^2$ ) every month, using a portable penetrometer. The sampling sites were selected with the same criterion used with the earth core sample.

*Black-faced Ibis abundance.* We quantified the number of Black-faced Ibises in the pastures during the nine month of the study by direct counting on either side of a 3100 m long transect with indeterminate width (Bibby *et al.* 1992). We surveyed the transect by vehicle for 45 minutes in the morning (between 09:00 to 10:00 h) on three consecutive days. We used this method because the Black-faced Ibis might be highly susceptible to human presence and, therefore, the transect could not be surveyed on foot. We determined the study area of the field using a Placom KP-80N digital planimeter and a topographic map (1:20,000 IGM, 1993). Monthly variation of ibis numbers, expressed as the arithmetic mean of birds in the study area, was evaluated between May and January.

*Statistical analysis.* A non-parametric test was used when data did not fit a normal distribution, otherwise we used parametric analyses.

Thus, for correlational analysis we used the Spearman rank-order correlation coefficient, and for multiple sample analysis we used a Kruskal-Wallis one-way analysis of variance (Zar 1984, Siegel & Castellan 1988). Given that search-time data fitted a normal distribution, we used a Tukey (HSD) test (Zar 1984) to detect temporal variation in searching time, comparing the Austral autumn (May) and winter (July) with the beginning of summer (December).

We determined Black-faced Ibis trophic preferences by comparing the frequency of occurrence of each prey type in the diet with the frequency of available prey using the goodness of fit test (Jaksic 1979, Dasgupta & Alldredge 2000). Positive significant differences were interpreted as prey preference (Jaksic 1979). Given that the Chi-square test fails to discriminate the preferred prey, we computed Bonferroni confidence intervals for the most represented prey in the feces (Neu *et al.* 1974, Byers *et al.* 1984, Schooley 1994, Dasgupta & Alldredge 2000, Dunstone *et al.* 2002).

To verify whether trophic opportunism in the Black-faced Ibis increased in the month when preferred prey items were scarce, we evaluated temporal variation in the trophic niche breadth over the periods May–August, September–October, November–December, and in January. We computed the Shannon-Wiener ( $H'$ ) Index to estimate trophic niche breadth (Krebs 1989, Moreno 2001). This index and its variance were calculated in the DIVERS program using natural logarithms (Franja 1993). In addition, we applied a Hutcheson  $t$ -test to evaluate differences in the index variances between periods of the year (Hutcheson 1970, Zar 1984).

## RESULTS

*Availability of invertebrates.* In terms of abundance, earthworms (*Lumbricus* spp.), black

cutworm larvae (*Agrotis* spp.), black pasture caterpillars (*Dalaca* spp.), and southern green chafers (*H. elegans*) were the most represented prey items in the pastures (Table 1). Mean abundance of these species varied significantly during the annual cycle (Earthworms, Kruskal-Wallis ANOVA,  $H = 166.95$ ,  $P < 0.001$ ; black cutworm, Kruskal-Wallis ANOVA,  $H = 77.66$ ,  $P < 0.001$ ; black pasture caterpillar, Kruskal-Wallis ANOVA,  $H = 83.99$ ,  $P = 0.001$ , and southern green chafer, Kruskal-Wallis ANOVA,  $H = 68.76$ ,  $P < 0.001$ ) and abundance was greater during the months with highest rainfall (May–September).

The mean total prey biomass varied significantly among months (Kruskal-Wallis ANOVA,  $H = 156.37$ ,  $P < 0.001$ ), reaching a maximum in September (Fig. 1). Southern green chafer and black pasture caterpillar were the invertebrates with greatest mean biomass contribution during the study period (Fig. 1). Neither ground hardness (Spearman,  $r_s = -0.455$ ,  $P = 0.306$ ) nor monthly precipitations (Spearman,  $r_s = 0.377$ ,  $P = 0.461$ ) correlated with variation in mean total biomass of potential prey available in the pastures during the nine months studied. Monthly precipitations and soil hardness decreased from September onwards, although soil hardness increased again during summer (Fig. 2). However, soil hardness did not correlate with monthly precipitation (Spearman,  $r_s = -0.543$ ,  $P = 0.266$ ).

*Diet and trophic preferences.* The Black-faced Ibis consumed a wide variety of prey during the months analyzed (Table 2). The larvae of the southern green chafer (Coleoptera, Scarabaeidae), black cutworm (Lepidoptera, Noctuidae), and black pasture caterpillar (Lepidoptera, Hepialidae) were the constituents that contributed most to the diet, although earwigs (*Forficula auricularia*) and beetles (family Carabidae) were also common in the feces.

The diet composition varied throughout the study period. Consumption of insect lar-

vae was not significantly correlated with consumption of the adult insects (Spearman,  $r_s = -0.217$ ,  $P = 0.576$ ). Subterranean insect larvae were abundant in the diet throughout the entire study period and a disproportionate high consumption of black cutworm was observed in January. The number of invertebrates species consumed by the Black-faced Ibis during the nine months studied increased from 6 prey types in the winter season to 12 in the summer period (Table 2). The trophic niche breadth was higher during late spring (November–December,  $HP = 1.646$ ,  $SD = 0.002$ ), when food abundance was low, than in winter (Shannon-Wiener, May–August  $HP = 1.259$ ,  $SD = 0.002$ ), early spring (September–October  $HP = 1.379$ ,  $SD = 0.003$ ), and summer (January,  $HP = 1.216$ ,  $SD = 0.001$ ).

Although the availability of the main prey items in the pastures was quite similar to diet composition, consumption of southern green chafer larvae, black pasture caterpillars, and black cutworms, as well as adult stages of unidentified species of Carabidae, was significantly greater than expected, considering their abundance in the pastures (Table 3). Preference for Carabidae was marked between September and December (Table 3). However, Carabidae might be underrepresented in the soil samples therefore this effect should be interpreted with caution.

*Consumption rate.* Consumption rate decreased significantly during the nine month study period (Kruskal-Wallis ANOVA,  $H = 116.296$ ,  $P < 0.001$ ). The highest consumption rate was in July and remained stable until October, when it started to decrease to its minimum in summer (January). The consumption rate correlated strongly and positively with prey availability (Spearman,  $r_s = 0.929$ ,  $P = 0.003$ ) and negatively with soil hardness (Spearman,  $r_s = -0.452$ ,  $P = 0.01$ ) (Fig. 3). In addition, ibises spent significantly more time searching for prey during summer

TABLE 1. Total number of invertebrates in monthly soil samples taken from the pastures near Chahuilco, Chile, between May 1999 and January 2000. (a) = adult stage, \* = prey with scarce representation in the soil samples.

Prey	May n = 54	June n = 80	Aug n = 39	Sep n = 39	Oct n = 39	Nov n = 39	Dec n = 39	Jan n = 39
<i>Agrotis</i> spp.	45	103	54	41	21	0	3	14
Asilidae	0	4	7	15	0	0	0	0
Carabidae (a)	2	8	6	2	0	3	1	1
Curculionidae	14	35	13	6	0	27	35	11
<i>Dalaca</i> spp.	8	127	17	4	1	20	0	5
Elateridae	7	39	18	20	15	48	5	3
<i>Hylamorphba</i> spp.	47	104	31	51	15	4	0	3
<i>Lumbricus</i> spp.	430	786	407	453	278	46	71	68
Tipulidae	0	0	0	0	0	0	0	19
Other prey*	2	5	2	6	1	2	0	1
TOTAL	555	1211	555	600	331	150	115	125

(December, mean = 39.37, SE = 7.69, n = 26) than during autumn (May, mean = 22.62, SE = 1.86, n = 67) and winter (July, mean = 21.4, SE = 1.76, n = 89) (Tukey HDS test<sub>q, 3, 182</sub> = 0.537,  $P = 0.004$ ).

*Black-faced Ibis abundance.* On average, we counted 179.6 (SE = 32.2) ibises during one observation tour. The population abundance showed an increase with a maximum in winter (July) followed by a progressive and sustained decline from September, reaching a minimum in December (Fig. 3). The number of ibises did not correlate with seasonal precipitations (Spearman,  $r_s = 0.543$ ,  $P = 0.266$ ) but was positively correlated with the overall invertebrate availability in the pastures (Spearman,  $r_s = 0.958$ ,  $P = 0.001$ ), and with abundance of black cutworm and southern green chafer larvae (Spearman,  $r_s = 0.905$ ,  $P = 0.001$  and Spearman,  $r_s = 0.929$ ,  $P = 0.001$ , respectively).

## DISCUSSION

Consumption and trophic preferences of the Black-faced Ibis for insect larvae were independent of ground hardness and monthly

precipitations, but positively correlated to variations in prey availability. This suggests that the specific life cycle of the prey (in particular insect larvae) generates an annual alternation in their population density and availability, which probably constitutes the main causal factor influencing the feeding ecology of the Black-faced Ibis in the study area. These results contrast with studies in humid tropical environments, where fluctuations in the hydrological conditions are a critical factor in prey availability, influencing the trophic components of wading birds (Kushlan 1981, 1986, Ausden *et al.* 2001, Lorenz *et al.* 2009, Beerens *et al.* 2011, Dorn *et al.* 2011, Herring & Gawlik 2013). In this environment, a reduction in rainfall intensity during the dry season causes the water level to recede, and fishes and aquatic invertebrates become concentrated into smaller, shallower pools. This seasonal fluctuation determines the foraging opportunities for many species of wading birds (Kushlan 1981, Dorn *et al.* 2011).

During our nine-month study, the diet of the Black-faced Ibis consisted mainly of soil macro-invertebrates, with a marked prefer-

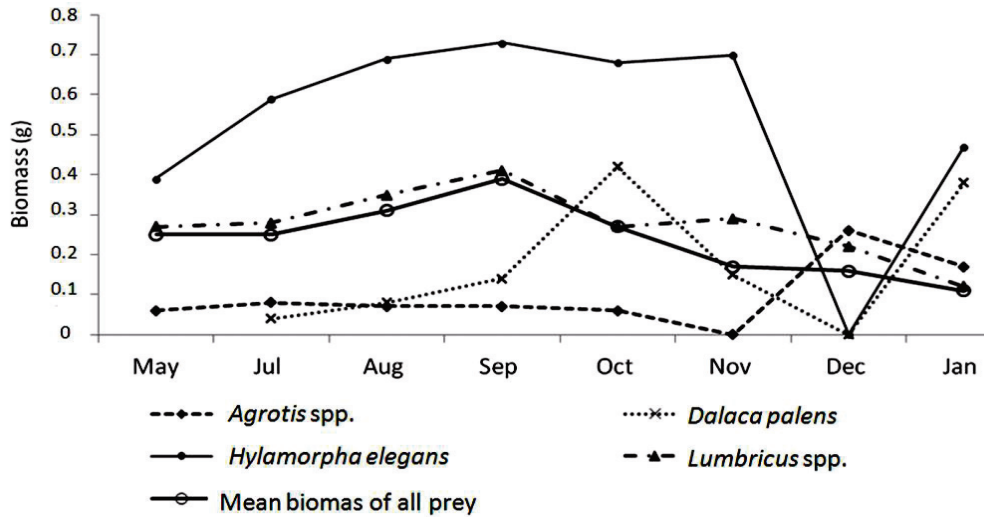


FIG. 1. Monthly variation in mean biomass (g) of all prey and for the four main prey items available to the Black-faced Ibis (*Theristicus melanoptis*) in the pastures near Chahuilco, southern Chile, between May 1999 and January 2000.

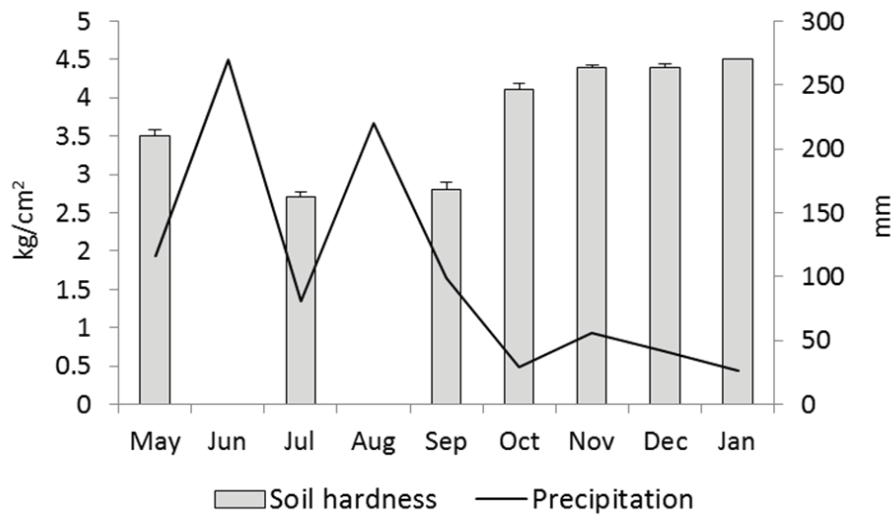


FIG. 2. Monthly variation of environmental variables, precipitation (total mm per month) and mean soil hardness (kg/cm<sup>2</sup>, ± SE), in the pastures near Chahuilco, southern Chile.

ence for insect larvae, although the preference varied throughout the year. However, we were unable to detect earthworms, which are an important diet component of the Black-faced

Ibis according to previous stomach-content analyses (Gantz 2010). This is most likely due to the fact that diet analyses using feces may be biased towards prey with indigestible

TABLE 2. Number and frequency of occurrence (in brackets) of different prey types present in the feces of the Black-faced Ibis (*Theristicus melanopis*) between May 1999 and January 2000, foraging in pastures near Chahuilco, Chile. (\*) = prey scarcely represented in the feces include: Curculionidae larvae, Dipterae larvae, and Formicidae.

Prey	May n = 11	June n = 34	July n = 41	Aug n = 43	Sep n = 42	Oct n = 42	Nov n = 41	Dec n = 44	Jan n = 39
<b>ADULT STAGES</b>									
Acruidae	11 (0.73)	0	0	0	0	0	1 (0.02)	8 (0.18)	37 (0.52)
Araneae	0	0	0	0	1 (0.02)	3 (0.07)	12 (0.29)	13 (0.30)	23 (0.52)
Carabidae	12 (0.55)	0	5 (0.12)	2 (0.04)	11 (0.26)	12 (0.29)	31 (0.59)	51 (0.66)	126 (0.93)
<i>Ceroglossus chilensis</i>	1 (0.09)	0	0	0	1 (0.02)	0	3 (0.07)	3 (0.07)	1 (0.02)
Curculionidae	1 (0.09)	0	0	1 (0.02)	2 (0.05)	0	0	3 (0.07)	10 (0.21)
Elaeidae	0	0	0	0	0	2 (0.05)	3 (0.07)	7 (0.11)	4 (0.02)
<i>Toxofila auricularia</i>	30 (0.82)	14 (0.26)	13 (0.29)	8 (0.16)	16 (0.24)	12 (0.24)	16 (0.29)	275 (0.48)	103 (0.83)
Hemiptera	0	0	0	0	0	2 (0.05)	0	7 (0.11)	10 (0.24)
<i>Hylamorpha</i> spp.	0	0	0	0	0	56 (0.21)	2 (0.05)	38 (0.66)	19 (0.43)
Total adults	55	14	18	11	20	87	68	405	333
<b>LARVAL STAGES</b>									
<i>Agritis</i> spp.	26 (0.64)	16 (0.35)	17 (0.29)	23 (0.22)	33 (0.41)	50 (0.45)	18 (0.29)	15 (0.34)	801 (0.98)
Curculionidae	5 (0.18)	5 (0.15)	0	3 (0.07)	2 (0.05)	0	2 (0.05)	0	0
<i>Dalaca</i> spp.	0	39 (0.44)	138 (0.58)	142 (0.78)	220 (0.83)	156 (0.81)	234 (0.71)	41 (0.50)	30 (0.38)
Elaeidae	0	3 (0.09)	1 (0.02)	4 (0.09)	2 (0.05)	2 (0.05)	0	9 (0.16)	6 (0.12)
<i>Hylamorpha</i> spp.	0	69 (0.47)	259 (0.83)	288 (0.86)	35 (0.38)	10 (0.21)	1 (0.02)	6 (0.07)	5 (0.12)
Total larvae	31	132	415	460	292	218	255	71	842
Other prey (*)	0	0	2 (0.05)	1 (0.02)	0	0	5 (0.07)	3 (0.05)	3 (0.05)
Not identified	0	0	0	0	0	10 (0.14)	12 (0.17)	7 (0.11)	0
Total prey	86	146	433	471	312	305	323	476	1175



TABLE 3. Variation in prey preferences of the Black-faced Ibis (*Theristicus melanopis*) in pastures near Chahuilco, southern Chile, between May 1999 and January 2000. \* =  $p < 0.05$ .

Prey	May–August		September–October		November–December		January	
	$\chi^2 = 737.39$ , $P = 0.001$		$\chi^2 = 8938.18$ , $P = 0.001$		$\chi^2 = 1681.48$ , $P = 0.001$		$\chi^2 = 980.46$ , $P = 0.001$	
	Bonferroni intervals for $p_i$	Jacob D Index	Bonferroni intervals for $p_i$	Jacob D Index	Bonferroni intervals for $p_i$	Jacob D Index	Bonferroni intervals for $p_i$	Jacob D Index
<i>Agrotis</i> spp.	0.056-0.099	-0.672	0.11-0.019	-0.493	0.045-0.116	0.615*	0.941-0.975	0.938*
Carabidae	0.007-0.029	-0.141	0.020-0.066	0.594*	0.149-0.253	0.799*	0.020-0.052	-0.655
Curculionidae	0.003-0.021	-0.781	-0.003-0.011	-0.807	-0.004-0.014	-0.987		
<i>Dalaca</i> spp.	0.265-0.339	0.195*	0.653-0.758	0.976*	0.613-0.735	0.857*		-1.000
Elateridae	0.001-0.015	-0.855	-0.002-0.017	-0.941	0.003-0.041	-0.924		
<i>Hylamorpha</i> spp.	0.543-0.623	0.581	0.053-0.116	-0.734	0.002-0.034	-0.235	-0.001-0.013	-0.886

structures vs. the detriment of soft prey, such as earthworms (Votier *et al.* 2003, Weiser & Powell 2011).

Variation in the feeding resources exploited, and in the feeding strategies used by the Black-faced Ibis, is in accordance with the predictions of the optimal foraging theory. One of these predictions is that in periods of resource scarcity birds can expand their diet, incorporating a greater variety of prey, while in periods of abundant food availability their diet is less varying and specialized on potentially high-quality prey (Krebs 1978, Wiens 1989, Todd *et al.* 1998, Begg *et al.* 2003, Beerens *et al.* 2011; Margalida *et al.* 2009, 2012; Herring & Gawlik 2013). According to these predictions, the pastures of the study area would offer high food availability during winter and early spring, and this could explain the more specialized diet and preferences of the Black-faced Ibis for insect larvae during these periods. On the contrary, decreased consumption rates and increased search times, considered to be reliable indicators of low prey availability in the environment (Collazo *et al.* 2010, Jahn *et al.* 2010), show that during late spring and summer food availability in the pastures is more limited. During this period, ibises show increased trophic plasticity,

incorporating a greater number of prey items into its diet, in particular adult surface-dwelling insects. The greater consumption of adult insects during this period, which are less profitable than their larvae for nutrition (Naef-Daenzer *et al.* 2000, Newell *et al.* 2014), is correlated with the lower availability of the latter in the pastures. Similarly, the greater consumption of surface-dwelling insects during months with lower food availability indicates that the Black-faced Ibis increases its foraging repertoire, using not only a tactile foraging strategy (i.e., to capture subterranean larvae) but also visual cues to capture surface-dwelling insects. This variation in feeding strategies has been documented in other species of birds that experience food limitations throughout the year (Wiens 1989, Todd *et al.* 1998, Begg *et al.* 2003, Beerens *et al.* 2011, Margalida *et al.* 2012, Herring & Gawlik 2013).

Changes in invertebrate abundance seem to be the main explanatory factor of ibis abundance during the nine months in the study area. This is evidenced by the close association between temporal reduction of total prey biomass, availability of the most profitable prey, and the concomitant decrease in the abundance of the Black-faced Ibis. The

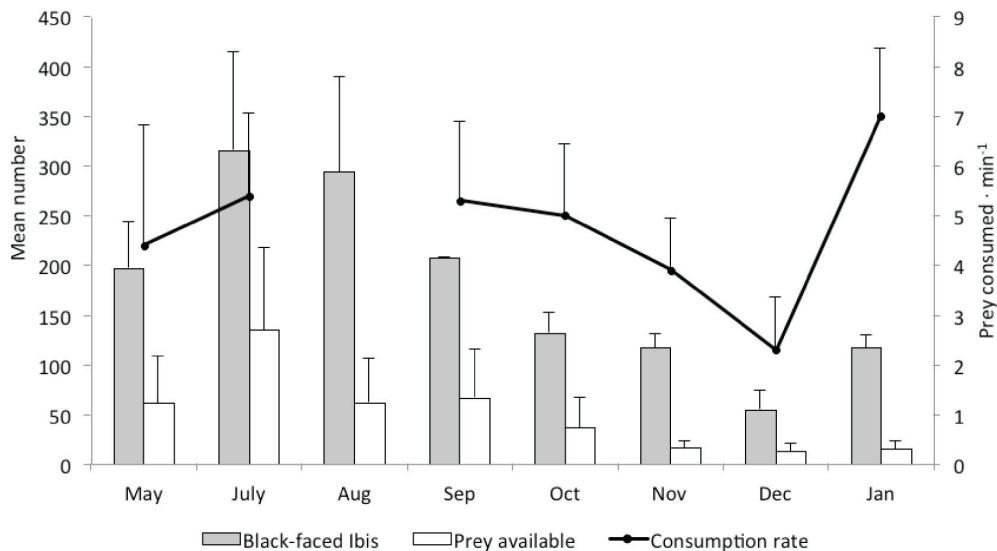


FIG. 3. Monthly variation of the mean number ( $\pm$  SE) of the Black-faced Ibis (*Theristicus melanopis*), consumption rate (prey consumed/min), and number of prey items available in pastures near Chahuilco, southern Chile, between May 1999 and January 2000.

reduction in the number of Black-faced Ibises in the pastures during the nine-month study period coincides with that reported for birds that adopt a “search strategy” (as opposed to an “exploiter strategy” *sensu* Beerens *et al.* 2011, Herring & Gawlik 2013). These birds abandon patches when food is scarce, to search for other, more productive ones (Herring & Gawlik 2013). Although reduced food availability may be the cause for reductions in ibis abundance (Gawlik 2002), establishing breeding territories may have similar effects on bird numbers. There is ample evidence that breeding territories limit the number of individuals in an area (Ridley *et al.* 2004, López-Sepulcre & Hokko 2005, Newton 2013). In particular, when food is scarce, the breeding territory is larger, and the territory holders defend it by excluding conspecifics, ultimately reducing bird density in the area. However, aggressive interactions during the breeding period are rare in the Black-faced Ibis, suggesting that this species does not

establish or defend breeding territories. Preliminary observations suggest that aggressive behavior seems to be restricted to small areas around the nest (AG unpub. data). Hence, we consider that the start of the breeding season is unlikely to constitute the main explanation for the decrease in the number of Black-faced Ibises in the study area.

To conclude, this study adds valuable data on the trophic ecology of this little-known Neotropical endemic ibis. It also contributes to a better understanding of the seasonal variation in trophic conditions as parameter for avian diet (Ramos *et al.* 2011). Additionally, due to current climate change, it is of increasing conservation concern to establish whether birds show flexible responses to seasonal changes (Fontaine *et al.* 2015) in food availability (Pearce-Higgins & Green 2014). Thus, we consider the information gathered in this study as relevant for future studies on the potential effects of climate change in temperate agro-ecosystems of southern Chile, using

the Black-faced Ibis as an appropriate avian model.

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