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Trophic Ecology of Breeding White-headed Steamer-Duck (*Tachyeres leucocephalus*)

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Abstract.—White-headed Steamer-Ducks (*Tachyeres leucocephalus*) are flightless waterfowl endemic to a small section of coastline in Patagonia, Argentina. This study provides the first detailed information on White-headed Steamer-Duck diet composition, foraging behavior and prey availability. This study was conducted in the northern San Jorge Gulf, Patagonia, during 2007. Fifteen feeding territories were identified, and food availability was quantified within them and also within unused areas. A total of 45 feces were analyzed to determine diet composition, and foraging behaviors of females were monitored. Benthic community diversity differed between territories and non-territories. Overall, diversity and invertebrate abundance tended to be higher in territories. Ten invertebrate prey taxa were identified in adult diets, and the most frequent prey in feces were crabs, mussels, and ragworms. Head-neck dipping was the most common method of feeding. Our results improve the understanding of the relationship between diet, selection of areas with special invertebrate availability and foraging techniques used to access and exploit the resources. *Received 1 July 2013, accepted 21 October 2013.*

Key words.—Chubut Steamerduck, diet, food availability, foraging behavior, Patagonia, *Tachyeres leucocephalus*, White-headed Steamer-Duck.

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White-headed Steamer-Ducks (*Tachyeres leucocephalus*) (formerly Chubut Steamerduck) are flightless marine waterfowl endemic to a 700-km section of coast of Chubut Province, Patagonia, Argentina (Agüero *et al.* 2012).The foraging ecology of White-headed Steamer-Ducks (steamerduck) has rarely been studied. Livezey (1989) analyzed the stomach contents of 34 individuals and found that mollusks and crustaceans were the main prey of steamerducks. In addition, little is known about their foraging behavior. Although reported to feed almost exclusively by diving (Weller 1972; Livezey and Humphrey 1984), Gatto *et al.* (2008) indicated that White-headed Steamer-Ducks mostly fed using a head-submergence technique. Finally, the availability and diversity of invertebrates in steamerduck foraging areas has never been examined. Additional information about the trophic ecology of White-headed Steamer-Ducks is needed to improve our understanding of important factors in foraging habitat selection and the underlying ecological factors that may influence the unusual natural history of this species.

Our objective was to study the trophic ecology of White-headed Steamer-Ducks by examining their foraging behavior and diet and determining the availability of prey in and outside feeding territories.

Methods

Study Area

Our study was conducted along 22 km of mainland coastline and six islands and islets in the northern San Jorge Gulf, Patagonia, Argentina (Fig. 1), where ~25% of the total estimated population of White-headed Steamer-Ducks is found (Agüero *et al.* 2012). We obtained behavioral data and collected benthic and fecal samples weekly during a period of 7 weeks (non-consecutive) from 2 October to 18 December 2007, during the incubating period for White-headed Steamer-Ducks (Agüero and García Borboroglu 2013).

Food Availability

We identified and determined the area of 15 intertidal sectors where White-headed Steamer-Ducks were observed foraging. These non-adjacent territories were located just offshore from where nests were located. During the incubation period when males were patrolling territories (Agüero and García Borboroglu 2013), we observed confused males that "steamed" across the surface water flapping their wings at their own female re-entering the territory after being chased away from the nest. Immediately, the territorial pair adopted an extreme form of the "alert" posture for a long time (about

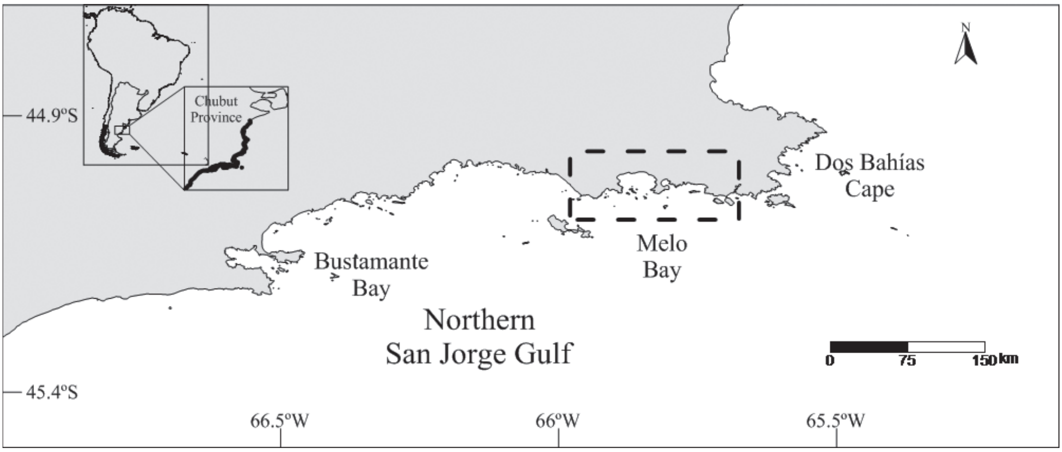

Figure 1. Coastal map of northern San Jorge Gulf showing the area where the foraging ecology of White-headed Steamer-Ducks (*Tachyeres leucocephalus*) was studied. In the inset map, breeding distribution in the Chubut Province is shown as a thick line.

30 min) swimming around the territory (see Moynihan 1958). Observations of this behavioral pattern allowed us to determine the extent of each pair's territory. We delineated territory boundaries using physical references of the landscape (i.e., headlands and exposed rocks), and we calculated distances and angles from these references to document territory boundaries and estimate their areas (Gauthier 1985).

Because White-headed Steamer-Ducks feed only during low tide (Gatto *et al.* 2008), we were able to access the feeding territories during spring tides when low tides were lower than average. To quantify food availability in 15 territories, we collected benthic samples using six randomly placed 15 x 15-cm quadrats in each feeding territory. We selected quadrat locations using tables of random numbers to generate *x* and *y* coordinates. We removed all invertebrates and algae from each quadrat using a scraper; we placed them in bags and preserved them in a freezer until analyzed. To examine differences in prey availability in territories and unused areas, we used the same sampling protocol in 15 areas that were not used by steamerducks. We selected these intertidal areas from the areas where we found no presence of White-headed Steamer-Ducks based on observations made during previous visits and surveys (Agüero *et al.* 2010, 2012).

In the lab, we passed samples through 1-, 0.5-, and 0.25-mm-mesh sieves. On a white tray, we picked out invertebrates retained by the 1-mm sieve and, using 10x magnifications, sorted the material caught by the 0.5-mm-mesh sieve. We found only sand and small gravel in the 0.25-mm sieve. We counted all invertebrates and identified them using published guides (Harrison and Ellis 1991; Boschi *et al.* 1992; Forcelli 2000), invertebrate collections at Centro Nacional Patagónico (CENPAT), and consulting taxonomists. We preserved a sample of hard body parts diagnostic of each identified invertebrate taxa in 70% alcohol and subsequently used these to identify food items in fecal samples.

Diet

We collected fecal samples around 15 nests where females were incubating. Because only females incubate (Agüero and García Borboroglu 2013), we collected fresh feces to ensure they corresponded to females. Only three fresh feces were found for some nests; therefore, we standardized the sample size to that amount. Each one was analyzed separately in the lab, but results were combined by nest in recognition that these were not independent samples and that our sampling unit was the female. We dried and stored collected fecal samples in plastic bags until they could be analyzed.

In the lab, we passed each fecal sample through 1-, 0.5-, and 0.25-mm-mesh sieves under tap water. We identified and counted at 8-64x magnification all fragments resistant to digestion and diagnostic of invertebrate taxa (e.g., gastric mill, jaws and mollusk shells). We identified fragments using Huespe (2005) and our diagnostic body parts collection.

Foraging Behavior

We collected foraging behavior data using focal observations of 29 females. Due to logistical constraints, we were only able to sample feeding territories and collect feces for 15 of 29 observed females. Observations were conducted from a fixed point on the coastline, allowing us to see the sampled females while avoiding being detected by them. Following the methods of Gatto *et al.* (2008), we observed them during low tide. Females were observed for 1 hr, with foraging behavior observed for periods of 10 min followed by periods of 5 min when birds were not observed. Observations were made using binoculars (10 x 40) or a spotting scope (25-40x). Each female was observed seven times during the breeding season (with at least 7 days between successive observations), with a total of 280 min spent observing each female.

We documented time spent using each of four feeding techniques (Gatto *et al.* 2008), including filtering (just the bill is under water), head-neck dipping (head and part of the neck is under water), up-ending (the front half of the body is submerged and only tail and legs are visible) and diving (entire body is submerged). We summed the number of minutes each technique was used by each female across all observation periods, and then determined the average number of minutes each technique was used by each female (n = 29).

Analysis

We determined differences in the benthic community between territories and unused areas using one-way analysis of similarities (ANOSIM test; Álvarez-Cabria *et al.* 2011). When ANOSIM results indicated differences, we evaluated the contribution of each taxa for mean dissimilarity between these groups using the SIMPER procedure (Clarke and Warwick 1994). We also compared prey abundance between territories and non-territories using t tests with Bonferroni corrections for multiple comparisons. Prey abundance was defined as the number of individuals of each taxon counted in all quadrats by territory.

We calculated frequency of occurrence (FO) and relative frequency (RF) for all food items found in the feces to describe the diet of adults. Frequency of occurrence was expressed as the number of times a given food item occurred in any of three fecal samples from a given female, whereas relative frequency was expressed as the ratio between the FO of each food item and the total frequency of all observed food items.

RESULTS

Territories (n = 15) ranged in size from 40 to 800 m^2 ($\bar{x}$ = 247.5 ± 59.9 m^2). We found significant differences in the benthic community between territories and unused areas (ANOSIM; R = 0.23, P = 0.001), and SIMPER analysis showed that seven taxa contributed more than 50% to those differences (Table 1). *Perumytilus purpuratus*, *Lasaea* spp., tanaids (Tanaidacea), isopods, and *Cyrtograpsus* spp. were most abundant in territories, accounting for 97.4% of the total fauna. In unused areas, 97.2% of the fauna consisted of *P. purpuratus*, *Lasaea* spp., and isopods. Overall, invertebrate abundance tended to be higher in territories, with significant differences for tanaids (Tanaidecea; P < 0.001) and *Cyrtograpsus* spp. (P = 0.01). However, after Bonferroni corrections (α = 0.002), only tanaid abundance was higher in territories (Table 1).

We identified 10 prey types in the diet of steamerducks, including seven mollusks (Mitilidae, *Lasaea* spp., Chiton, *Trophon* spp., *Actionidae* spp., *Fissurella* spp., and *Nacella magellanica*), two crustaceans (isopods and *Cyrtograpsus* spp.), polychaetes (Nereiididae), and unidentified organic matter (green, red, and brown algae). Prey most often found in feces were *Cyrtograpsus* spp. (15 sampling units, RF = 0.16), Mitilidae (13 sampling units, RF = 0.14), and Nereidiidae (13 sampling units, RF = 0.14).

Head-neck dipping was the most common foraging technique used by female steamerducks (143.1 ± 10.8 min, 51.1% [of 280 min sampled per female]), followed by filtering (88.2 ± 12.6 min; 31.5%), diving (47.6 ± 7.0 min, 17%), and up-ending (1.1 ± 0.1 min, 0.4%). Dives were short in duration, with birds generally under water < 30 sec (16 ± 6 sec; n = 75 dives by nine individuals).

DISCUSSION

Of 10 food items identified in the diet of White-headed Steamer-Ducks, the most frequent prey were *Cyrtograpsus* spp., Nereididae, and Mitilidae. However, fecal analysis may be subject to biases because softer, more easily digestible components of the diet are under-represented (Anderson *et al.* 2008). Prey selected by adult steamerducks were not the most abundant prey, suggesting that abundance of consumed prey may be more relevant for understanding habitat quality for White-headed Steamer-Ducks than overall abundance of benthic invertebrates.

Several authors have suggested that food resources are defended by some territorial species of ducks (Nudds and Ankney 1982; Livezey and Humphrey 1985). However, some investigators have reported little evidence to support the food hypothesis, where food supply for adults and nestlings is the major function of territoriality (Patterson 1982; Gauthier 1985). We did not quantify a relationship between food availability and territory size or breeding success, but did find differences in benthic community between used and unused areas. Notably, the most abundant invertebrate in feeding territories was not detected in the diet

Table 1. Average abundance (± SE) of available invertebrates in territories of White-headed Steamer-Ducks and unused areas. Prey that contributed > 50% to dissimilarity between used and unused areas (SIMPER) are underlined. Tanaidacea abundance was significantly higher in territories (in bold).

	Territories	Unused Areas	
Prey Item	Mean Number of Individuals		P^*
Tanaidecea	**75.5 ± 15.1**	**11.8 ± 4.0**	**0.003**
Cyrtograpsus spp.	38.3 ± 8.5	12.6 ± 4.0	0.011
Lasaea spp.	248.3 ± 34.4	141.3 ± 39.3	0.050
Nacella magellanica	17.1 ± 8.5	0.9 ± 0.3	0.067
Isopoda	75.2 ± 18.1	68.9 ± 19.6	0.820
Crepidula spp.	16.3 ± 6.1	2.3 ± 1.4	0.033
Aulacomya ater	5.6 ± 2.7	7.5 ± 3.8	0.680
Perumytilus purpuratus	1,719.6 ± 299.6	1,187.3 ± 238.9	0.180
Mytilus chilensis	2.3 ± 1.1	2.5 ± 0.9	0.880
P. purpuratus seeds	989.3 ± 256.8	616.7 ± 160.1	0.230
M. chilensis seeds	9.1 ± 5.7	1.6 ± 0.5	0.200
A. ater seeds	5.5 ± 2.8	4.3 ± 1.7	0.720
Chiton	0.9 ± 0.2	1.4 ± 0.4	0.320
Trophon spp.	0.7 ± 0.3	2.0 ± 0.4	0.022
Actionidae spp.	11.9 ± 2.6	5.7 ± 1.3	0.040
Fissurella spp.	2.4 ± 0.8	0.7 ± 0.3	0.056
Amphipoda	4.3 ± 2.8	1.9 ± 0.7	0.420
Betaeus spp.	4.4 ± 2.9	1.4 ± 0.8	0.320
Asteroidea	1.7 ± 0.4	1.1 ± 0.5	0.350
Nereididae	1.3 ± 0.9	0	0.150
Total abundance	48,445	31,076	
Species richness	20	19	

*α value (0.0025) based on Bonferroni corrections for multiple comparisons.

of steamerducks. Some possible explanations for this are that small crustaceans are quickly and almost completely digested and, thus, are under-represented or absent in fecal samples (Swanson and Bartonek 1970), or tanaids could not be prey for adults, but they may be prey for ducklings (Johnsgard 1978). Even though this study provides the first evidence of higher diversity of benthic community and invertebrate abundance in territories, additional research is needed to evaluate the hypothesis of territoriality as a food defense.

McKinney (1965) hypothesized that the degree of territoriality by species in the family Anatidae was a function of the defendability of food resources. Most duck species using seasonal feeding areas where food supply cannot be feasibly defended exhibit little territorial behavior (Talent *et al.* 1982; Duebbert and Frank 1984). Conversely, species with strong territorial defense, like steamerducks (Livezey and Humphrey 1985), occupy more predictable and stable environments such as estuaries, rivers, or permanent wetlands (Savard 1984; Gauthier 1985). White-headed Steamer-Ducks have a restricted distribution in an area where weather and physical conditions are proper for recruitment and development of abundant intertidal food resources (Hidalgo *et al.* 2007; E. Schwindt, pers. commun.). In this regard, strong territoriality of White-headed Steamer-Ducks may be related to the defense of predictable and abundant food resources, although this has not been explicitly addressed.

We found that feeding methods other than diving, especially head-neck dipping and filtering, were commonly employed by female White-headed Steamer-Ducks. Intertidal areas where steamerducks feed are characterized by dense beds of mussels harboring a diverse assemblage of small mobile invertebrates (Bertness *et al.* 2006; Hidalgo *et al.* 2007). In this case, steamerducks probably catch crabs or ragworms by head-neck dipping when these invertebrates leave the shelter or by removing Mitilidae from bottom substrate using the bill with a heavy nail. Furthermore, algae, like kelp beds, provide a protected environment for small mobile animals (Barrales and Lobban 1975). Steamerducks probably feed on these algae filtering on the exposed laminae during low or rising tides, or diving in deeper water (Johnsgard 1978; Livezey 1989).

The frequency of dives in our study was similar to that reported by Gatto *et al.* (2008). In addition, we occasionally found that diving by steamerducks was linked to the presence of kelp beds, consistent with the findings of Johnsgard (1978) and Livezey (1989). In accordance with Livezey (1989), we believe the relatively infrequent dives observed for steamerducks in our study may be due, in part, to the sparseness of kelp beds in the area.

This study provides the first detailed information about key aspects of the foraging ecology of White-headed Steamer-Ducks. It improves our understanding of the relationship between diet, the selection and defense of areas with special invertebrate availability and the foraging techniques used to access and exploit the resources. However, more detailed information on trophic ecology throughout the year, as well as for ducklings and juveniles, is needed. Additional studies should assess the effects of food availability on demographic variation and further address the role of food resources in territorial behavior, spatial segregation and population density regulation.

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