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ENVIRONMENTAL FACTORS INFLUENCING HABITAT USE OF SOLITARY AND PAIRED TORRENT DUCKS (*MERGANETTA ARMATA*) IN NORTHWESTERN PATAGONIA, ARGENTINA

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ABSTRACT.—The Torrent Duck (*Merganetta armata*) is one of the four species of ducks that live in fast flowing rivers, and the only one inhabiting mountain rivers from Venezuela to Argentina. This study examines physical-chemical and biological environmental variables associated with different stages of the annual cycle of this waterfowl, to test the relationship between environmental variables and the establishment of territories by Torrent Ducks in the southern part of their range between November 2009 and April 2011. Territories were defined as sites where a pair of Torrent Ducks was found throughout the year, while non-territories were defined as sites where solitary birds were spotted in some seasons but not year-round. The variables that best explained the habitat use by Torrent Ducks were: 1) in spring, the energy of main prey items available per square meter of river, and 2) in fall, the flow rate. Higher food availability in spring and higher water flow in small rivers in fall were associated positively with paired Torrent Ducks' territory establishment. The future assessment of breeding success in territories with contrasting levels of food and water flow may allow for the determination of the importance of these variables for habitat selection, and the meaning that changes in precipitation caused by climate change may have on this species. *Received 24 June 2016. Accepted 19 December 2016.*

Key words: Andean rivers, habitat quality, management measures, *Merganetta armata*, Patagonian parks, river flow, threatened species, Torrent Duck.

Degradation and loss of habitat are the greatest threats to wild bird species (International Union for Conservation of Nature [IUCN] 2015). Therefore, there is a need for understanding changes in bird habitats (Block and Brennan 1993, Holmes and Sherry 2001) and how to prioritize habitat conservation (Johnson 2007). Distinction among the terms habitat, habitat quality, habitat use, and habitat selection are often unclear in bird studies (Hall et al. 1997, Jones 2001). The term habitat refers to a set of physical environmental factors that a species uses for its survival and reproduction (Block and Brennan 1993). Higher quality habitats are those expected to promote survival and reproduction because of a particular set of environmental factors (Hall et al. 1997). The habitat use relates to the actual distribution of individuals across habitat types, while the habitat selection refers to a hierarchical process of behavioral responses that result in the disproportionate use of some habitats (Hutto 1985). Thus, habitat use patterns are the result of habitat selection processes (Jones 2001).

The Torrent Duck is one of four waterfowl river specialists in the world (Carboneras 1992). It inhabits white-water mountain rivers in the Andes range from southern Argentina and Chile to Venezuela (Carboneras 1992). Across its range, Torrent Ducks may be found in areas with very different characteristics, such as cold forests, temperate rainforest, and even arid steppes and its altitudinal range spans 4500 m a.s.l., to sea level (Carboneras 1992). This diversity of range-wide habitat suggests that local populations may differ in the features that are important in the habitat use process. Although the IUCN (2015) considers the Torrent Duck to be a species of Least Concern globally, it recognizes that some local populations are declining. In Argentina, the Torrent Duck has been classified as Threatened (López-Lanús et al. 2008). Competition and predation by introduced species such as salmonids and the American mink (*Vison vison*) have been suggested as possible causes for its decline (Cerón and Trejo 2012), but other factors may also be important.

The presence and abundance of a species in a given habitat are needed to establish patterns of habitat use; however, these factors are not sufficient to establish habitat quality, as density and breeding habitat quality may not be correlated positively (Van Horne 1983, Hobbs and Hanley 1990, Bock and Zach 2004, Johnson 2007). For

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example, in territorial birds such as Torrent Ducks, some individuals of reproductive age may be found in habitats of lesser quality (so-called floaters), where they do not breed, particularly when favorable habitat is scarce. Hence, their presence may lead to the conclusion that a site has high quality when it does not. Factors such as the reproductive status of the individuals and environmental variables have to be considered to assess habitat quality (Van Horne 1983, Johnson 2007). In order to breed, paired Torrent Ducks need to establish a year-round territory 0.7–2 km in length (Naranjo and Ávila 2003). This territory consists typically of a mixture of rapids, waterfalls, and pools where this monogamous species feeds on immature stages of benthic aquatic insects, and these features may suggest the existence of good habitat quality.

Some authors have previously studied the distribution of Torrent Ducks in order to determine negative effects of anthropogenic disturbance (Sardina Aragón et al. 2011, Pernollet et al. 2013), and a positive effect of food availability (Álvarez et al. 2014) and water flow (Sardina Aragón et al. 2011, Pernollet et al. 2013, Álvarez et al. 2014) on the habitat use. However, these studies focused solely on the abundance of ducks and did not distinguish between floaters and territorial pairs. It is therefore still unknown what environmental cues are better related to habitat quality and are probably sensed by paired Torrent Ducks when they are establishing a breeding territory.

Our aim was to study several environmental variables related to habitat use by Torrent Ducks in order to distinguish breeding pairs from floaters in southern Argentina. Our hypotheses were: (i) habitat use by Torrent Ducks is explained by a number of environmental variables, and (ii) habitat use by paired Torrent Ducks (territories) is related to better environmental conditions than habitat use by floaters (non-territories).

METHODS

Study Area

Fieldwork was carried out along white-water rivers in Nahuel Huapi National Park, located in northwestern Patagonia, Argentina (40° 46′–41° 35′ S, 71° 49′–71° 10′ W, Fig. 1). Average annual temperature in the area is 10 °C with hot dry summers and annual rainfall ranges from 500–3,500 mm, concentrated mainly as rain and snow during winter (Mermoz et al. 2009). The surface area of the park is 710,000 ha and includes a wide variety of habitats, with 14 vegetation types (as described by Mermoz et al.2009). The altitude of the park is 400–3491 m a.s.l., increasing westwards. The mountains have steep slopes, forming a landscape with white-water streams and valley rivers with sections of rapids flowing from woodland areas to the steppe (Mermoz et al. 2009).

To evaluate features related to habitat use, we randomly selected 20 out of 26 sites where Torrent Ducks were recorded by National Parks Technical Delegation staff from 1997–2005 (Fig. 1). Each site consisted of sections of rapids $\geq$900 m long, which is long enough for a Torrent Duck's territory to be located within each section (Carboneras 1992). These sites represented 78% of all records of Torrent Ducks in Nahuel Huapi. Territories were defined as sites where a pair of Torrent Ducks was found throughout the year. Non-territories were defined as sites where solitary birds were spotted, or feces were recorded, in some seasons but not year-round (Cerón et al. 2010), or sites with previous sightings (Administración de Parques Nacionales 2014) but without current occupation. Between 2006 and 2011, seven sampled sites classified as territories were monitored two to six times per year, and 13 sampled sites classified as non-territories (Fig. 1) were monitored eight times per year, to ascertain the presence of individual Torrent Ducks (or their feces) (Fig. 1). Because surveys were performed in 8 years in different seasons, and feces are abundant when Torrent Ducks are present (GC, pers. obs.), it is unlikely that territories have been misclassified as non-territories.

Measured Environmental Variables

Field work was carried out in 3 years during two seasons: 1) spring (Nov 2009, Dec 2010), which represents the period of duckling hatching and the highest water flow, and 2) early fall (May 2010, Apr 2011), the time when juveniles become independent (Cerón 2012) and water flow is lower.

In spring and fall, at each site rapids were divided into 30-m long sections. The number of

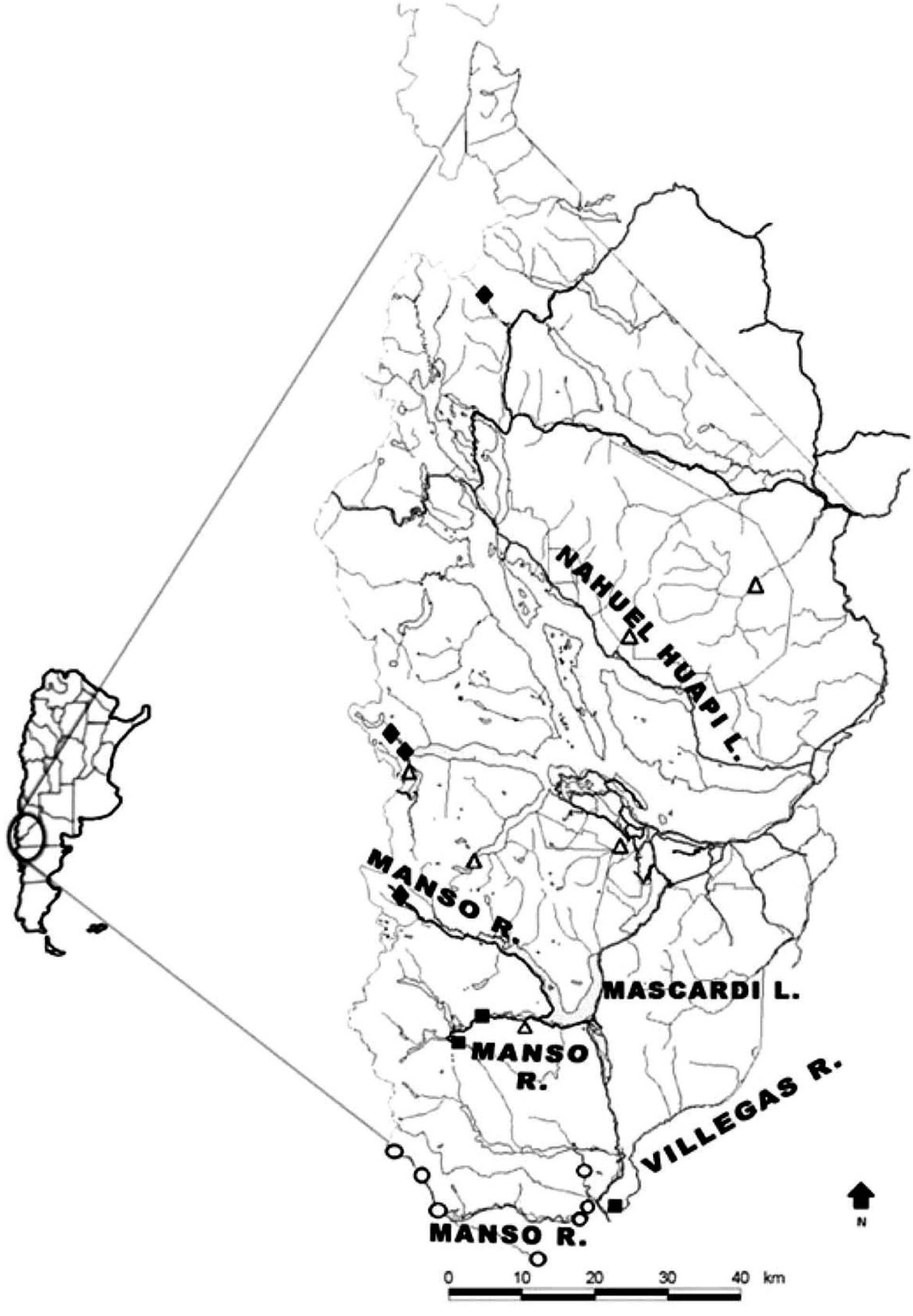

FIG. 1. Sampling sites in Nahuel Huapi National Park. Territories: squares (large rivers), diamonds (small rivers); non-territories: circles (large rivers), and triangles (small rivers). L = Lake; R = River.

sections depended on the rapid length which was ~1 km, (i.e., ~30 sections). Then, one section was randomly selected for estimation of the following variables: water depth (m), water body width (m), current speed (m/s), pH, energy density of main prey (kJ/m^2), substrate type, and number of emerging rocks (modified from Rodway 1998).

To measure river depth and width, five transects perpendicular to the water course were randomly placed within each 30-m long section. We took total width measurements along each transect. To measure depth, we divided each transect into five equal sections and obtained five estimations at each transect's central point, averaging the measures. Current velocity was estimated with a digital water velocity meter (Global Water FP111), and flow rate was calculated by multiplying river width by depth by current velocity. Water pH was measured with a pH meter (Hanna HI 9023, Scinteck Instruments, Manassas Park, VA, USA).

To distinguish among substrate types, the riverbed was categorized into five categories based on visual observations: 1) gravel, 2) small rocks (rocks 10–20 cm in diameter), 3) medium rocks (20–40 cm), 4) large rocks (>40 cm), and 5) rocky platform. Then, we visually determined the percentage of riverbed which corresponded to each substrate type in each sampling site. This variable was measured only once at each sample site, because it does not vary between seasons.

In order to estimate the energy density of main prey, we sampled aquatic invertebrates by imitating Torrent Ducks' two feeding strategies, either 'scraping' or 'searching' technique (Cerón and Boy 2014). To sample invertebrates that Torrent Ducks may capture using the 'scraping' feeding technique, 0.09 m^2 of big boulders (>40 cm diameter) were brushed on the top, sides, and downstream faces. To sample invertebrates that Torrent Ducks may capture with the 'searching' feeding technique, 0.09 m^2 of river bed (rocks <40 cm diameter) were removed, and the small rocks were brushed into a Surber net (0.09 m^2, 1-mm mesh) held downstream in the current. The 'scraping' and the 'searching' feeding techniques were imitated on five randomly selected locations 0.09 m^2 from each 30-m long section, per site and sampling date. The number of invertebrates per m^2 was estimated by dividing sampled invertebrates per 0.45 m^2 (I/m^2). This was performed for invertebrates sampled by the 'scraping' (I_{sc}/m^2) and 'searching' (I_{se}/m^2) sampling techniques. Then, the available invertebrates per m^2 (AI/m^2) for a 30-m stretch was calculated as:

$$(\mathrm{AI/m^2}) = (\mathrm{I_{sc}/m^2}) \cdot \text{proportion of large rocks} + (\mathrm{I_{se}/m^2}) \cdot \text{proportion of small rocks}$$

In the Nahuel Huapi National Park, the main prey items of Torrent Ducks are four taxa of aquatic insects (>80%): species in the family Simuliidae of the Order Diptera, *Smicridea*, species of the Order Trichoptera, species in the family Gripopterygidae of the Order Plecoptera, and species in the subfamily Atalophlebiinae of the Order Ephemeroptera (Cerón et al. 2010, Cerón and Boy 2014). We collected all individuals of these taxa from water. We counted, weighed, and then dried them at 60 °C for 48 hrs. Dried samples were weighed again, finely ground, and pellets were made using a press (Parr Instrument Co. 2812, Moline, IL, USA). The caloric content of each sample was obtained by burning pellets in a micro-bomb calorimeter (Parr Instrument Co. 1425. Moline, IL, USA). The values obtained were corrected for ash and acid content and expressed as energy values (kJ/g ash-free dry weight; Boy et al. 2009). Then, the energy per gram of invertebrate (kJ/AI) was obtained.

Finally, the energy density of main prey (E) for each site was calculated as:

$$\mathrm{E} = (\mathrm{AI/m^2}) \cdot \mathrm{kJ/AI}$$

All variable data were averaged per sample site and per season (2 consecutive years), and their effect on the presence of Torrent Ducks' territories was tested.

In order to randomly select sites or measurement points along stream reaches, we always used the random number function in a scientific calculator.

Statistical Analysis

As Torrent Ducks defend their territories year-round (Carboneras 1992), a territory in spring will remain a territory in fall unless there are negative changes in environmental conditions. Thus, we did not analyze seasons as a factor that may have an effect on presence/absence of territories but studied the relationship between the presence/absence of territorial individuals and changes in environmental variables (e.g., a river with optimal features during spring may not be a territory because the environment became suboptimal in fall). In this study, we used season to temporally stratify data, reducing variance, so data from spring and fall were always analyzed separately. Two different analyses were performed to assess a) the effect of environmental variables and the energy density of main prey on the presence of territories (multiple regression test) and b) the effect of water flow on the presence of territories (two sample *t*-test).

Effects of Environment and Prey.—In order to limit multicollinearity, two variance inflation factor (VIF) analyses were performed among variables (Graham 2003), one for spring and another for fall. We removed variables with VIF values >5. In both seasons, the number of emerging rocks (VIF = 8.73), speed (VIF = 7.63), width (VIF = 7.89), and depth (VIF = 7.92) were eliminated because they were collinear. The emerging rock variable was collinear with depth and water flow; while speed, depth, and width were collinear with the water flow variable. Therefore, variables included in models were the energy contribution of main prey per m^2 of river, submerged small rocks, gravel, flow, and pH.

For spring and fall, multiple regression tests were performed assuming a binomial distribution with a logit link function. The presence (1) or absence (0) of a territory was analyzed among 20 sites considering the assessed variables. All possible models with VIF pre-selected variables and their combinations were tested, and ordered by Akaike's Information Criterion for small sample sizes (AIC_c) (Sugiura 1978, Hurvich and Tsai 1989), and associated weights were calculated (Wagenmakers and Farrell 2004). When differences between the null and studied models' AIC_c exceeded 2, the model with the lowest AIC_c and the highest weight was selected.

Effects of Water Flow.—During fall, at the end of the dry season, there is a sharp decline in the water levels of the rivers in the study area that could be a limiting factor for Torrent Ducks. Many studied sites were on big rivers where water speed, depth, and width are high all year, this may hamper the detection of a water flow effect on the presence of territories by the multiple regression that included all the sampled sites. So, we stratified our data, performing separate multiple regression in small and large rivers, defined by its river order (Strahler 1957). In this study, we have considered small rivers those with a river order from 1–2, and big rivers those with a river order >2. As data subsets were too small to perform separate regression analyses per season and river size (e.g., in spring four territories and six non-territories were found in small rivers, and three territories and seven non-territories were located in big rivers), we tested the existence of differences between territories and non-territories for water flow with two sample *t*-tests. The distribution for big river data was normal and homoscedastic, so two sample Student's *t*-test (significance at $P = 0.05$) was performed. However, small river data could not adjust a normal distribution, possibly because of a high variance (e.g., water flow range = 0.29–6.54 m^3/s, for small rivers in fall). Then, a Mann-Whitney *U*-test (significance at $P = 0.05$) was used for small rivers (Mann and Whitney 1947).

RESULTS

Habitat Use

The pH was close to neutral (7.3 ± 0.2; mean ± standard deviation) in spring, at the beginning of the breeding season. The water body width, depth, and current velocity varied widely among sampling sites, both within territories and between territory/non-territory sites (Table 1). In fall, at the end of the dry season, the pH presented a general trend towards greater acidity (6.7 ± 0.3). As for substratum size, a higher contribution of large rocks to the total river bed was observed in territories than in non-territories, for small (terr. = 0.3 ± 0.1 and non-terr. = 0.17 ± 0.06) and big rivers (terr. = 0.24 ± 0.09 and non-terr. = 0.3 ± 0.1) (Table 2).

In spring and fall, the regression analysis showed that the physical-chemical environmental variables were not related to territory/non-territory categories (Table 3). In spring, the better supported multiple regression models for Torrent Ducks' habitat use were all positively related to the energy density of main prey items. In fact, all best regression models included this variable (Table 3). In fall, the best supported model was the null model. However, a competing model with the lowest AIC_c was presented by the model including

TABLE 1. Mean depth, width, speed, flow, pH, and energy contribution of main prey items per m^2, taken at the sampling sites in large and small rivers in spring and fall, classified as territory or non-territory (non territ.) of Torrent Ducks in Nahuel Huapi National Park. Numbers in parentheses = standard deviation. E = energy contribution of main prey per m^2 of river. N = number of replicates.

Season	Category	River Size	Depth (m)	Width (m)	Speed (m/s)	Flow (m^3/s)	pH	E (kJ/m^2)	N
Spring	Territory	Small	0.5 (0.1)	10 (4)	1.3 (0.7)	8 (6)	7.3 (0.1)	2 (1)	4
	Non territ.	Small	0.5 (0.2)	13 (7)	1.5 (0.2)	10 (8)	7.2 (0.2)	0.9 (0.7)	6
	Territory	Large	2 (1)	38 (16)	1.8 (0.5)	135 (82)	7.45 (0.07)	1.5 (0.4)	3
	Non territ.	Large	2 (1)	39 (11)	2.3 (0.7)	240 (118)	7.4 (0.2)	0.7 (0.5)	7
Fall	Territory	Small	0.42 (0.09)	10 (2)	1.1 (0.4)	4 (2)	6.8 (0.1)	10 (15)	4
	Non territ.	Small	0.4 (0.1)	5 (2)	0.6 (0.3)	1 (1)	6.8 (0.4)	3 (3)	6
	Territory	Large	1.1 (0.3)	24 (15)	1.6 (0.9)	55 (71)	6.80 (0.08)	17 (20)	3
	Non territ.	Large	1.3 (0.6)	28 (8)	1.8 (0.4)	66 (32)	6.8 (0.4)	6 (4)	7

only energy contribution of main prey per m^2 of river, as we observed in spring (Table 3).

River Water Flow

When small rivers were analysed separately, in fall territories were found to have higher flow levels than non-territory sites ($U_9 = 1$, $P = 0.02$) but not in spring ($U_9 = 9$, $P = 0.52$). Whereas for big rivers, no significant differences in water flow between territories and non-territories were detected in fall ($t_8 = 0.34$, $P = 0.74$) or in spring ($t_8 = 1.39$, $P = 0.20$).

DISCUSSION

In white-water rivers of northwestern Patagonia, the establishment of territories by pairs of Torrent Ducks was best explained by a high energy contribution of the main prey available per m^2 in spring. In small rivers in fall, the highest flow rate was found in territories of paired Torrent Ducks.

Regarding food availability, the better supported multiple regression models for Torrent Ducks' habitat use were all positively related to energy density of the main prey items in spring, however, this relationship was not found in fall. Primary production is the main source of organic matter in valley rivers (Cummins 1974). In northwestern Patagonia, strong currents prevent the growth of algae and aquatic plants, especially during the time of year with higher flow (spring). Therefore, in spring, the river communities of aquatic insects depend on less abundant sources of organic matter (Lampert and Sommer 2007), which may reduce abundance of the macroinvertebrates. This would explain the importance of food availability for the establishment of paired Torrent Ducks' territories during this season. In addition, the flow of large rivers did not seem to affect the establishment of territories both in spring and in fall, possibly because these rivers are big enough to support a territory during the period of low water levels (fall). As for small rivers, a higher water flow was detected in paired Torrent Ducks' territories than stream reaches that supported solitary birds, in fall but not in spring. This may be explained by the decline in river water flow observed in fall for small rivers.

Our results agree with those from a study of two streams in the Central Andes where the presence of

TABLE 2. Means (standard deviation) of substratum divided into rocky platform, gravel (rocks <10 cm in diameter), small rocks (10–20 cm), medium rocks (20–40 cm), and large rocks (>40 cm); taken at sampling sites in large and small rivers, classified as territories or non-territory (non territ.) of Torrent Ducks in Nahuel Huapi National Park.

Category	Size	Rocky platform	Large rocks	Medium rocks	Small rocks	Gravel
Territory	Small	0.3 (0.3)	0.3 (0.1)	0.3 (0.1)	0.1 (0.1)	0.07 (0.08)
Non territ.	Small	0.02 (0.06)	0.17 (0.06)	0.29 (0.09)	0.3 (0.1)	0.2 (0.1)
Territory	Large	0.3 (0.3)	0.24 (0.09)	0.3 (0.1)	0.1 (0.2)	0.05 (0.08)
Non territ.	Large	0.1 (0.2)	0.3 (0.1)	0.3 (0.1)	0.2 (0.1)	0.1 (0.1)

TABLE 3. Habitat variables included in null, full, and 10 better models for spring and the best model including variables (BMV) for fall, showing the associated degrees of freedom (df), Akaike's information criterion (AIC_c), and weight (W). Int.: Intercept; E: energy contribution of main prey per m^2 of river; RP: rocky platform; LR: large rocks, MR: medium rocks, SR: small rocks; G: gravel. The estimated values of the parameters are given for the model with the best fit, SE in parentheses.

	Model	Variables	df	AIC_c	W	Int.	b1
Spring	Null		1	27.9	0.14	-	-
	Full	RP + LR + MR + SR + G + Flow + Ph + E	9	30.3	0.003	-	-
	1	E	2	20.7	0.41	3.62 (1.57)	2.3 (1.1)
	2	E + pH	3	21.9	0.22		
	3	E + Flow	3	22.2	0.19		
	4	E + Flow + pH	4	22.8	0.14		
	5	E + Flow + pH + LR	5	28.3	0.01		
	6	E + pH + Flow + RP	5	29.3	0.005		
	7	E + pH + Flow + MR	5	29.4	0.005		
	8	E + pH + Flow + MR	5	29.5	0.005		
	9	E + pH + Flow + G	5	29.7	0.004		
	10	E + pH + Flow + SR	5	29.7	0.004		
Fall	Null		1	27.9	0.18	-	-
	Full	RP + LR + MR + SR + G + Flow + pH + E[1]	9	30.5	0.003	-	-
	BMV	E	2	26.7	0.33	-	-

ducks (breeders and floaters considered altogether) was best explained by food availability and water flow (Alvarez et al. 2014). In addition, Sardina Aragón et al. (2011) studied the distribution of Torrent Ducks in two streams of the North Argentina Andes to determine that the highest density was found in the highest water flow river. Finally, Pernollet et al. (2013) studied two rivers with hydroelectric production finding a positive correlation between duck densities and water flow. Hence, food availability and water flow appear as the most important environmental factors in determining Torrent Ducks' habitat use. However, we studied 16 streams and showed that these factors are not only important for the presence of Torrent Ducks but for the presence of territories. That is to say, paired Torrent Ducks are more likely to be found in habitats with higher food and water current than solitary Torrent Ducks (floaters).

Unlike other waterfowl, which are mainly migratory, Torrent Ducks are residents (Carboneras 1992). Nevertheless, mountain rivers, where this species lives, are dynamic environments, with significant variations in annual flow. Strong increments in the water flow may obligate Torrent Ducks to abandon their territories by removing the riverbed thereby decreasing available food (Cerón 2012, Pernollet et al. 2013), while decrements in the flow may make the environment uninhabitable by Torrent Ducks (possibly because current fails to provide refuge against predators). When this is the case, large fast-flowing rivers that can buffer the effects of water level variations could become high quality habitats. On the other hand, bigger substratum size could be more stable during floods, reducing the negative effect on food availability.

As Torrent Ducks are strongly territorial, when selecting a river reach in which to breed and defend, they have to consider environmental clues that refer not only to present habitat characteristics but also indicate future conditions. Our results suggest that it is as important that a territory provide good food availability as that it guarantees a proper water flow year-round. The observation of pairs of Torrent Ducks in rapid river reaches that are abandoned after a few months (Pernollet et al. 2012; G. Cerón, pers. obs.) may be related to the premature selection of a site, which after some time did not provide necessary conditions to establish a territory.

Climate change is expected to alter rain/snow precipitation and snow/glacier melting in the Andean region (Vera et al. 2006). Then, as precipitation changes river flow, climate change may modify habitat availability for Torrent Ducks over their entire range of distribution. In years when winter snowpack is low, there may not be enough flow in small streams during the dry season. On the contrary, accelerated glacier melt or heavy rainfall (especially in deforested areas) can cause floods that are capable of leading to mortality of ducks (as in Pernollet et al. 2012). According to our results of food availability and flow being important for the establishment of territories, precipitation extremes could cause Torrent Ducks to abandon territories.

Our study evaluated several habitat features related to habitat use by Torrent Ducks to provide information that may be useful for decision-making by conservation groups. We found that paired Torrent Ducks are more likely to establish in habitats with higher food in spring and water current in fall than solitary Torrent Ducks (floaters). Then, it might be that several thresholds in food availability and water flow exist for (i) the presence of ducks, (ii) the establishment of territories by pairs, and (iii) the successful breeding of Torrent Ducks. If future studies estimate an optimal food availability and water flow for the successful breeding of Torrent Ducks, we could say that both variables are proxy for habitat quality and likely important during habitat selection.

American minks were present in all our study sites (G. Cerón, pers. obs.) and may be playing an important role in the presence of territories, as rivers with proper food availability but without territories have been observed. For the New Zealand river specialist Blue Duck (*Hymenolaimus malacorhynchos*), the importance of predation risk for the presence of territories is well established (Godfrey 2003). A long-term study on the effect of introduced predators such as the American mink, and salmonids as potential food competitors or modifiers of aquatic invertebrate communities, may help to develop a better model for understanding why in some cases, flow and food availability were not sufficient to explain habitat use by Torrent Ducks in South Argentina.

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