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## Relationships among territory size, body size, and food availability in a specialist river duck

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### ABSTRACT

Models of territorial behaviour predict a reduction in territory size when food availability and competitive pressure increase. Moreover, body size can play an important role in territorial defence. The Torrent Duck (*Merganetta armata*) is a river specialist that exhibits year-round territorial behaviour and long-term pair bonds. Food availability measured as biomass of invertebrates per unit area, territory and body size of Torrent Ducks were studied in the Andes in Argentina to test predictions of territoriality models. The availability of aquatic invertebrates decreased with latitude, while territory size increased. As expected, territory size of Torrent Ducks showed a negative relationship with the availability of aquatic invertebrates, a major food source for Torrent Ducks. Larger males and females paired together and occupied territories with greater food availability. Body size may be important for both males and females for the successful acquisition and defence of territories, especially during the non-breeding season when the contest winner acquires or maintains the territory and the mate. Our results suggest that Torrent Duck specialisation on fast-flowing mountain rivers leads to year-round territoriality in both sexes, a positive correlation between territorial defence and body size, and territory size proportional to food availability and population density.

### ARTICLE HISTORY

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### KEYWORDS


Andes range; food availability; *Merganetta armata*; mountain rivers; territorial behaviour; territorial defence; Torrent Duck

### Introduction

Relationships among food availability, foraging efficiency and territory size have been a central issue in ecology for decades (Brown 1964; Andersson 1978; Adams 2001; López-Sepulcre and Kokko 2005). Territory is defined as an area occupied almost exclusively by an animal or group of animals by means of excluding other members of the same species, directly via contest competition or indirectly via advertisement (Wilson 1975). For many species that exhibit food-based territoriality, where food resources are distributed homogeneously in space and time, there is considerable disparity in individual territory sizes (Carpenter *et al.* 1983; Norman and Jones 1984; Mares and Lacher 1987; Marshall and Cooper 2004). For such species, having larger territories, increase their access to greater absolute amounts of feeding (i.e. energetic) resources. However, territory size can reach an optimum beyond which defence, and movement (e.g. foraging or commuting) become overly costly (Andersson 1978).

Optimal foraging models predict a decrease in territory size with increasing food and competitor density (Schoener 1983), with these predictions being supported experimentally in a wide variety of taxa (Adams 2001). Many studies involving different vertebrate taxa have assessed the effect of food supply on population dynamics and found that with the addition of food, territory size usually decreases and population density increases (Sinclair 1989; Boutin 1990; Grant *et al.* 1998; Newton 1998; Royama 2012). Nevertheless, models of optimal territory size may not be applicable when animals defend contiguous territories (Adams 2001), because such models do not consider interactions among neighbours in their mathematical definitions. Unlike the non-contiguous situation, where the unoccupied space between territories allows territory holders to expand their defended area, contiguous territory holders defend smaller areas than their non-contiguous optimum, as a result of the pressure exerted by their neighbours (Hixon 1980; Grant 1997; Adams 2001).

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Territorial species invest part of their energy and time defending their territories from conspecifics (Petrie 1984; Price 1984; Bart and Earnst 1999; Candolin and Voigt 2001). Energy investment in defence should be related to food resources and probably territory size. In some territorial species, larger individuals have advantages over smaller individuals when defending their territories, and a positive relationship has been described between bird size and territory size and/or quality (Quinard *et al.* 2014). Some birds can even adjust their territory sizes as a function of gained weight (e.g. Carpenter *et al.* 1983).

Worldwide, four species of anatids are river specialists that inhabit fast-flowing montane rivers: the Blue Duck (*Hymenolaimus malacorhynchos*) from New Zealand, the African Black Duck (*Anas sparsa*) from sub-Saharan Africa, Salvadori's Teal (*Salvadorina waigiensis*) from New Guinea, and the Torrent Duck (*Merganetta armata*) from South America (Eldridge 1986a). Although they are not closely related (Livezey 1986), all river-specialist ducks are monogamous, exhibiting strong territorial behaviour and long-term pair bonds. Williams and Mckinney (1996) suggest that these behaviours may be adaptations to life in such specialised habitats. The Torrent Duck lives in fast-flowing rivers, in the Andes Range from Venezuela to southern Argentina (Carboneras 1992). Pairs defend river sections consisting of a mixture of rapids, pools, and waterfalls, generally of 1–2 km in length (Moffett 1970), although there is a high variability in territory sizes. In Colombia, for example, territories as small as 200 m in length have been recorded (Cardona and Kattan 2010). Torrent ducks establish territory boundaries at specific locations such as emergent rocks. The locations of territorial boundaries are fixed year-round, even during the breeding season. At these boundaries, pairs from contiguous territories perform territorial displays many times per week when their neighbours are present (Moffett 1970; Cerón 2012). As has been reported for other avian species with long-term pair bonds and year-round territorial defence (e.g. Hall and Peters 2008; Quinard and Cézilly 2012), both males and females contribute to the defence of territories (Eldridge 1986b).

Torrent Duck territories are narrow strips along riverbeds, and are defended year-round at only two boundaries (upstream and downstream) by both members of the pair. Territories can thus only vary in one dimension, constituting an interesting model system to assess the relationship between food abundance, male and female body size, and territory size. Territorial displays seem energetically expensive (Eldridge 1986b), and the larger the territory, the more energy is required to defend it. We therefore expect larger territories to be defended only when smaller ones are lacking in resources to sustain the pair. In other words,

we predict that territory size will be negatively correlated with food density, as the optimal models predict.

In order to explore factors affecting the territory size of Torrent Duck pairs, we conducted a study evaluating (i) the latitudinal variation in territory size and food resources over 25 degrees across the southernmost distribution of the species, and (ii) whether variation in the territory size of Torrent Ducks is related to food availability. In addition, we tested the hypothesis that larger male and female ducks will have territories with higher food density, assuming that a larger body size is advantageous for defending territories during intra-sexual confrontations. If this last hypothesis is true, there will be a positive correlation between the body sizes of paired males and females. Understanding the mechanisms involved in territory delimitation and defence could provide new information on ecological traits that lead to territoriality.

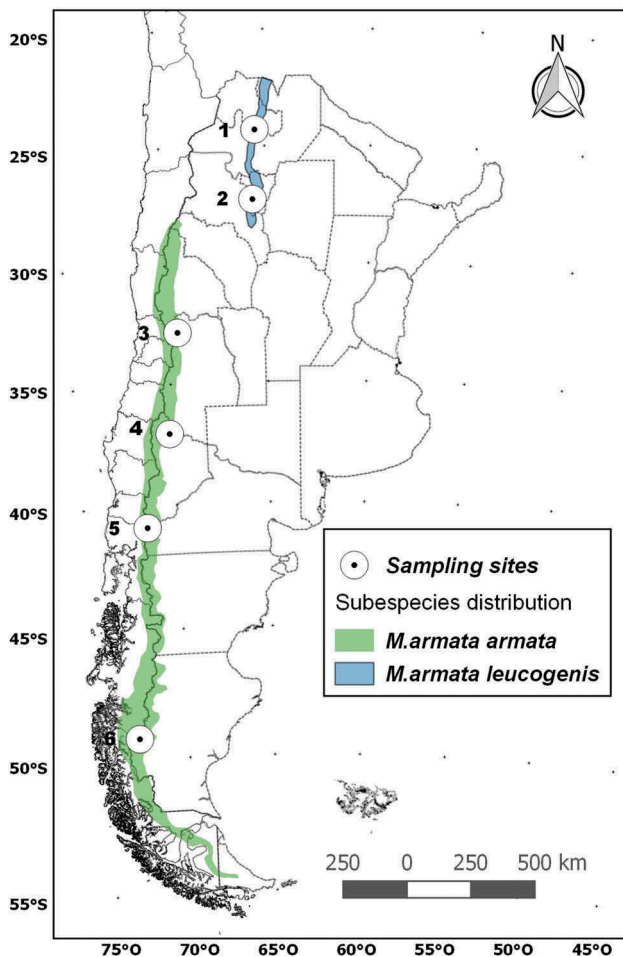
## Methods

### Study area

Fieldwork was carried out in Torrent Duck territories located in fast-flowing rivers, spanning almost the entire latitudinal range of the species in the Argentinian Andes (24°7' S–49°8' S). Four regions representative of the environments inhabited by Torrent Ducks in this area were selected, and a total of 25 territorial pairs were sampled (Table S1; Figure 1). In the northern region, Torrent Ducks inhabit rivers in the Andean montane forest known as southern Yungas, where the mean annual precipitation is 2000 mm and the average annual temperature is 13.9°C (Brown *et al.* 2005). In the central-north region, the mean annual precipitation (mostly snow) is 600 mm, and the mean annual temperature is 14°C (Abraham and Martínez 2000). In the central-south region, samples were taken in the temperate austral forest. The mean annual precipitation is 1800 mm, concentrated mainly as rain and snow in winter, while summers are dry. The average annual temperature is 14°C (Mermoz *et al.* 2009). The southern region consists of cold austral forest, where the average annual precipitation is 1500 mm, distributed year-round, with a greater concentration of rain and snow in the winter and an average annual temperature of 7.5°C (Cabrera 1976).

### Fieldwork

Field data were collected during the breeding season (i.e. austral spring–summer), from September to December 2014–2015, within a month of duckling hatching, and only in territories where ducklings were present (i.e.



**Figure 1.** Torrent Duck (*Merganetta armata*) subspecies distribution and sampling areas in the Argentinian Andes: 1 and 2: north region; 3 and 4: central-north region; 5: central-south region; and 6: south region.

successful territories). We considered only successful territories in order to ensure stability in their size and location, since recently established territories could change in size or be abandoned during the following months (Cardona and Kattan 2010). During the breeding season, territorial behaviour reaches its highest level in the year (Cerón 2012). Hatching takes place in October in the northern region, November in the central regions and December in the southern region. A single observer (G. Cerón) collected all samples and took all measurements, in order to minimise potential measurer effects.

### Food availability

Torrent Ducks feed on benthic aquatic invertebrates in fast-flowing rivers (Naranjo and Ávila 2003; Cerón and Boy 2014), with males and females feeding at the same microsites. They use two feeding techniques, either

using their beak to scrape the top, side, and downstream surfaces of large rocks to remove adhered invertebrates, or searching for invertebrates on the riverbed at the bottom and between small rocks (hereinafter ‘scraping’ and ‘searching’ techniques; Cerón and Boy 2014).

To estimate food availability, we collected aquatic invertebrates, endeavouring to imitate Torrent Duck feeding strategies (see below) according to the proportion of substratum types (which determines the proportion of taxa in each site), and territory size (total square metres) as in Cerón and Boy (2014).

In each territory, a flexible 0.09 m<sup>2</sup> square-frame was placed on 15 randomly selected sites of two different substrates to sample invertebrate availability (totaling an area of 1.35 m<sup>2</sup> within each pair territory) according to the following Torrent Duck feeding strategies: (1) ‘Scraping’: 0.09 m<sup>2</sup> of large boulders (>40 cm diameter) were brushed on the top, sides and downstream faces. (2) ‘Searching’: 0.09 m<sup>2</sup> of river bed (rocks <40 cm diameter) were removed, and the small rocks were brushed into a Surber net (0.09 m<sup>2</sup>, 1 mm mesh) held in the downstream current. The number of aquatic invertebrates per square metre sampled by the ‘scraping’ ( $I_{sc}/m^2$ ) and ‘searching’ ( $I_{se}/m^2$ ) sampling techniques was estimated by dividing sampled invertebrates ( $I$ ) by 1.35 m<sup>2</sup> ( $I/m^2$ ). Invertebrate availability per square metre for each territory ( $AI/m^2$ ) was calculated as:

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

In each territory, the proportion of submerged small (<40 cm diameter) and large (>40 cm diameter) rocks was estimated visually for 100 m sections of the river until the entire length of the territory was covered, and the values were averaged.

Invertebrates were identified at family or genus taxonomic level according to Merritt and Cummins (1997) and Fernández and Dominguez (2001). Invertebrates of each taxon from food-availability samples were counted and their fresh weight determined (0.01 mg) to estimate biomass per square metre. Items not found in faeces (see below) or not reported in the literature as eaten (Naranjo and Ávila 2003; Cerón and Boy 2014; Vera *et al.* 2014) were excluded from the calculations to estimate food availability. A reference collection was made using invertebrates’ head capsules, legs and/or mandibles from food samples to compare with sclerotised body parts resistant to Torrent Duck digestion, and this was used to determine diet composition.

To determine the prey items eaten by the Torrent Duck, 10 faeces were collected per territory in rivers with one territory, and four faeces per territory in rivers with three territories. These faeces were collected at the same places and times as the food samples. Fresh faeces were collected from emergent boulders and identified by size (approximately 2.5 cm long) and content (large proportion of sand and small pebbles mixed with invertebrates), which differentiates them from droppings of other birds in the study area (which are small or composed mostly of uric acid). Dry faeces were avoided in order to reduce losing sample material due to weathering. Collected faeces were preserved in 80% alcohol pending laboratory analysis. Faeces were disaggregated under a stereoscopic microscope and prey items were identified by comparison with the reference collection. It was assumed that faeces were dropped by territorial birds and not by floaters, since Torrent Ducks are very intolerant of intruders, especially during the breeding season, and quickly evict floaters from their territories. Territorial individuals seldom leave their territories, which ensures that they feed in the sampling area (Cerón 2012).

### **Individual traits and territory size**

In each territory, mist nets (black nylon, 100 mm mesh size, 2 m in height, 9–12 m in width) were placed across the river, near the location of the territorial pair. We waited for captures in camouflaged locations near to the net, quickly removing any captured duck. Each duck was banded using Darvic rings (size 9 mm) and identified by a colour code. Once marked, culmen length was measured from the beginning to the end of the cornea structure on the upper side of the beak, using a calliper (accuracy = 0.05 mm), after which the bird was released. As culmen length is positively related to other body size measurements in Torrent Ducks (Gutiérrez-Pinto *et al.* 2014), we used this trait as an estimator of body size. Body weight can be an inaccurate estimator of body size, because ducks may be captured wet or dry, with males usually captured dry, and females, which commonly swim or dive, usually captured wet (Alza *et al.* 2017; Cerón pers. obs.), which can result in biased data.

To determine territory boundaries, after ringing the ducks we watched them from camouflaged spots located near the suspected territory limits during the breeding season (based on the presence of different pairs). Duck pairs perform territorial displays many times per week at territory boundaries (i.e. emergent rocks), confronting the contiguous pair. We watched

for these display events until we were able to identify the precise limits between territories (i.e. displays were performed more than three times at the same spots, never trespassing these boundaries). This methodology was replicated at both upstream and downstream boundaries of each territory. In addition, some territories were monitored for several seasons or several years (as part of other studies), and these boundaries were maintained even when one member of the pair was replaced. In the case of territories located in isolated rapids, ducks were similarly watched from spots located in the transitional section between rapids and calm waters, to ensure that territorial individuals used only the rapids section of the river. Torrent Ducks spend several hours standing on emergent rocks, where coloured rings are easy to see with binoculars. Each boundary location was recorded using a GPS (eTrex Vista® HCx). To estimate the territory size of Torrent Ducks, the territory length was measured using Google Earth Pro (7.1.8.3036, 2015). River width was estimated by averaging 10 randomly selected widths per territory, measured with a 50 m measuring tape.

### **Data analysis**

This study is structured at three levels of analysis: (i) individual level (including inter-sex variation), (ii) territory level, and (iii) the relationship between individual and territory characteristics. We explored different relationships analytically, using linear mixed-effect models (LMM; Bolker *et al.* 2009) because of the hierarchical structure of our data (i.e. one pair per territory, territories nested in rivers, and rivers nested in regions).

#### **Individual level**

To describe body size and the differences between sexes, we compared culmen length in males and females including sex as categorical explanatory variable, culmen length as response variable, and territories, rivers and regions as random factors. In addition, we calculated the coefficient of variation (CV in percentage) of culmen length for males and females.

We correlated the culmen length between paired male and female ducks. Since residuals were non-homogeneously distributed, we used a generalised least squares (GLS) model which allows heterogeneity by including a weight function (Zuur *et al.* 2009). Different weight functions of variance were included in models, one at a time, maintaining constant response and explanatory variables. We selected as

the best model the one with the lowest value of Akaike information criterion corrected by the small sample size (AICc; Zuur *et al.* 2009). The second-best model had  $\Delta AICc > 2$ , so we did not consider it in our results (Burnham and Anderson 2004). In the selected model, the variance was modelled as a power of the male culmen length (weights function varPower), because residual values decreased with increasing male culmen length. This function allowed us to solve the problem of variance heterogeneity for a LMM (Zuur *et al.* 2009).

### Territory level

In the first model for this section we explored how the biomass of invertebrates per unit area (i.e. response variable) varied with latitude, including latitude as explanatory variable, and rivers as random factor (regions were excluded here in testing the effect of latitude). To test the hypothesis that territory size is affected by food availability, we constructed a second model, including the territory size as response variable and the biomass of invertebrates per unit area as explanatory variable, including rivers in regions as random factors. As biomass and latitude were strongly correlated (see results from the first model), latitude was excluded from this model in order to avoid multicollinearity effects (Zuur *et al.* 2009).

We explored whether territory size varied as a function of latitude through a model including territory size as response variable, latitude as explanatory variable, and river as random factor. Because normality and homogeneity of variance assumptions were not met, we modelled variance using different weights function of variance (Zuur *et al.* 2009), and compared the different models via the AICc criterion. The selected model included the function varFixed. The second-best model had a  $\Delta AICc > 2$ , so we did not include it in our results (Burnham and Anderson 2004). The selected model does not calculate a new parameter, but assumes a positive relationship between variance of territory size and latitude.

### Relationship between individual and territory characteristics

To test the prediction that larger ducks can obtain and maintain larger territories, we conducted an analysis including culmen length as explanatory variable and territory size as response variable. This analysis was performed for both sexes separately (to avoid collinearity between culmen length and sex; see results below), and included rivers and regions as random factors. In

order to analyse the variation in duck sizes in response to food availability, the variation in culmen length was modelled including the biomass of available food per unit area and sex as explanatory variables. In this model, territories were nested in rivers, and rivers in regions to account for the non-independence of the individuals from the same territory (breeding pair), from the same river, and from the same region.

In all analyses, biomass per unit area of available food was transformed via natural logarithm to achieve normality and homogeneity of the residuals; interpretation and figures are based on the transformed variable. In LMM analysis, the proportion of variance explained by explanatory variables (marginal  $R^2$ ), and by both explanatory and random effects (conditional  $R^2$ ) was calculated, following Nakagawa and Schielzeth (2013). Data analyses were performed with R 3.4.0 (R Core Team 2016), using nlme, bbmle and MuMIn packages. Data are provided as mean  $\pm$  standard deviation (SD).

## Results

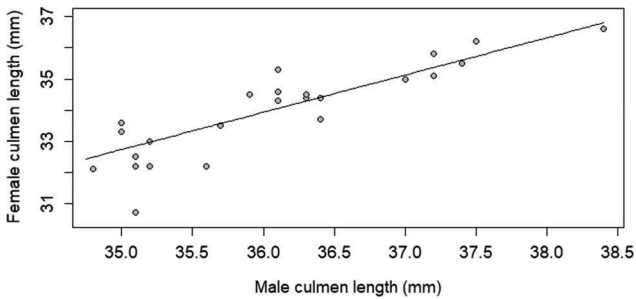
Twenty-five adult male and 24 female ducks from 25 territories in 11 rivers were captured in two consecutive breeding seasons during 2014–2015 (in one territory we failed to capture the female).

### Individual level

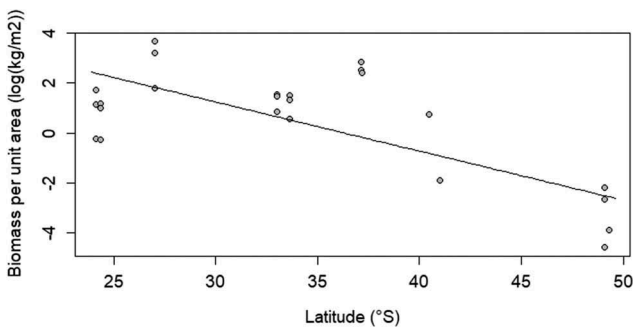
The culmen length of Torrent Ducks was larger in males ( $36.03 \pm 0.99$  mm; range: 34.60–38.40 mm) than in females ( $33.97 \pm 1.48$  mm; range: 30.70–36.60 mm;  $F_{1, 23} = 175.23$ ;  $p < 0.0001$ ). Male culmen length was on average 6.34% longer than female culmen length. Females had higher variability than males in culmen length (CV = 4.4 vs. CV = 2.7). The culmen length of paired males and females was positively correlated ( $t = 11.30$ ,  $p < 0.0001$ ,  $df = 22$ . Pearson correlation = 0.88) (Figure 2).

### Territory level

Torrent Duck territories were highly variable in size, food availability and proportions of substratum type (supplementary material Table S2). The mean territory size of a duck pair was  $7173.96 \pm 3425.66$  m<sup>2</sup> (range = 2992–15 120 m<sup>2</sup>). The mean estimated total food biomass was  $36.22 \pm 54.51$  kg per territory (range = 0.12–226.15 kg). The available invertebrate biomass per unit area averaged  $6.03 \pm 9.12$  g/m<sup>2</sup> per territory (range = 0.01–39.25 g/m<sup>2</sup>). The mean percentage of small rocks present in the river substratum was



**Figure 2.** Relationship between culmen length of paired males and females in Torrent Ducks: correlation equation: female culmen length =  $-9.16 + 1.20 \times \text{male culmen length}$ ; Pearson  $R = 0.88$ . See supplementary material S3 for parameter estimates.



**Figure 3.** Latitudinal variation in biomass of available food (invertebrates) per unit area ( $\log(\text{kg}/\text{m}^2)$ ) in the four sampling regions in the Argentinian Andes: density of food =  $7.15 - 0.20 \times \text{latitude}$ ; marginal  $R^2 = 0.53$ , conditional  $R^2 = 0.90$ . See supplementary material S3 for other parameter estimates in this model.

$45.6 \pm 20.0$  (range = 0–95), and the mean percentage of large rocks was  $54.4 \pm 20.0$  (range = 5–100).

Invertebrate availability decreased as latitude increased ( $F_{1, 9} = 13.99$ ;  $p = 0.005$ ; Figure 3). The marginal  $R^2$  was 0.53, while the conditional  $R^2$  was 0.90. Territory size showed a negative relationship with invertebrate availability ( $F_{1, 13} = 9.67$ ;  $p = 0.008$ ; Figure 4(B)). The marginal  $R^2$  for this model was 0.38, while the conditional  $R^2$  was 0.75. The territory size of Torrent Ducks increased with increasing latitude ( $F_{1, 9} = 5.46$ ;  $p = 0.044$ ; Figure 4(A)). The marginal  $R^2$  was 0.48, and the conditional  $R^2$  was 0.98.

### Relationship between individual and territorial characteristics

Culmen length was not related to territory size for either males ( $F_{1, 13} = 0.15$ ;  $p = 0.706$ ; marginal  $R^2 < 0.01$ , conditional  $R^2 = 0.58$ ) or females ( $F_{1, 12} = 0.001$ ;  $p = 0.941$ ; marginal  $R^2 < 0.01$ , conditional  $R^2 = 0.54$ ; Figure 5).

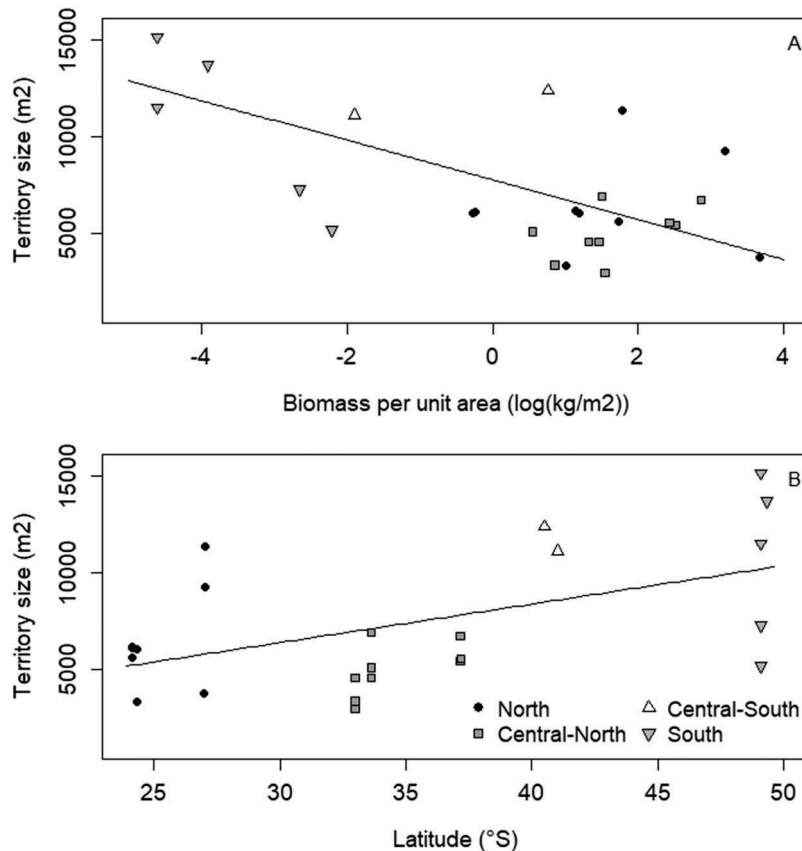
Culmen length was larger in territories with higher invertebrate availability ( $F_{1, 13} = 7.80$ ;  $p = 0.015$ ; Figure 6). There was no significant interaction between sex and invertebrate availability on the culmen length ( $F_{1, 22} = 3.41$ ;  $p = 0.078$ ; marginal  $R^2 = 0.48$ , conditional  $R^2 = 0.95$ ).

### Discussion

Torrent Duck territory size varied considerably, increasing with latitude, over the 25 degrees of latitude that we studied. The availability of aquatic prey species decreased with latitude, as expected for invertebrate biomass and densities in river systems (Cummins 1974; Rosenzweig 1995). The inverse relationship observed between territory size and biomass of the main food source for Torrent Ducks suggests that the availability of aquatic invertebrates is a relevant factor influencing the maintenance and defence of territories through optimal foraging behaviours. Finally, as expected, in our study area, larger males were paired with larger females, occupying territories with higher food density, i.e. better quality territories.

Territory is usually defended by male birds, particularly in species in which males are larger than females (e.g. Price 1984; Hyman *et al.* 2004). However, although male Torrent Ducks are approximately 6% larger than females (Carboneras 1992), both sexes engage in territorial defence (Cerón 2012). Positive correlations between body size and territory size (Adams 2001; Woodward *et al.* 2005), or between male body size and territory quality have been recorded in several bird species (e.g. Bart and Earnst 1999). However, we found no relationship between body size and territory size for the Torrent Duck, despite the positive relationship between body size and food availability.

During the breeding season, male and female Torrent Ducks defend their territories together, regardless of the intruder's sex. However, during the non-breeding season, males fight only with males and females only with females, without the support of their mates, which will remain in the territory with the contest winner (Cerón 2012). Body size can play an important role in territorial encounters in birds (e.g. Petrie 1984; Price 1984; Bart and Earnst 1999), and, although we did not conduct experiments to assess directly whether body size is decisive in defining the winner of each encounter, we found that larger ducks defended territories with higher invertebrate availability. If body size is advantageous in territorial encounters for both males and females, and since re-pairing mostly involves intra-sexual confrontations (Cerón



**Figure 4.** Variation in territory size of Torrent Duck breeding pairs in the Argentinian Andes in response to (A) biomass of available food (invertebrates) per unit area ( $\log(\text{kg}/\text{m}^2)$ ): territory size =  $7768.64 - 1023.79 \times \text{biomass per unit area}(\log)$ ; marginal  $R^2 = 0.38$ , conditional  $R^2 = 0.75$ ; and (B) latitude: territory size =  $429.76 + 198.87 \times \text{latitude}$ ; marginal  $R^2 = 0.48$ , conditional  $R^2 = 0.98$ . See supplementary material S3 for other parameter estimates in this model.

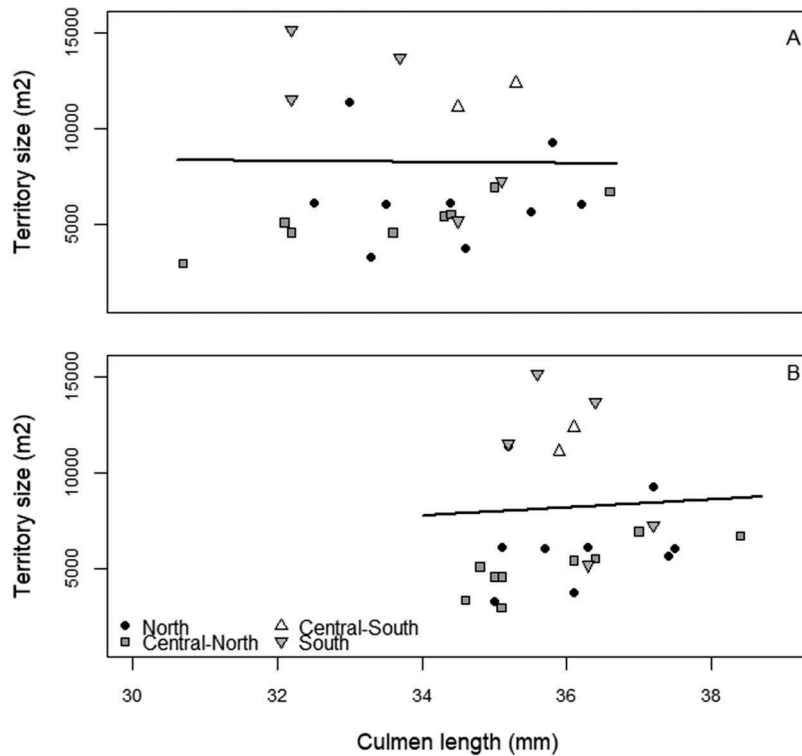
2012), a positive correlation between male and female body size should occur. Larger body sizes would thus allow for better quality territory, with access to a better quality mate (Erikstad *et al.* 1993; Hepp *et al.* 1993). In addition, beaks play a significant role during Torrent Duck territorial displays (Moffett 1970; Úbeda *et al.* 2007), suggesting that beak length could be an honest signal of individual quality (Zahavi 1975; Quinard *et al.* 2014). Therefore, we suggest that intra-sexual territorial confrontations expressed by males and females during the non-breeding season (Cerón 2012), with advantages for larger body sizes, could explain why larger male and female Torrent Ducks were paired together.

The size of territories defended by Torrent Ducks was highly variable and negatively related to food availability, as expected in animals that display food-based territoriality (Carpenter *et al.* 1983; Norman and Jones 1984; Mares and Lacher 1987; Marshall and Cooper 2004), and is predicted by the optimal foraging models. According to these models, territory size is also expected to decrease with increasing competitor

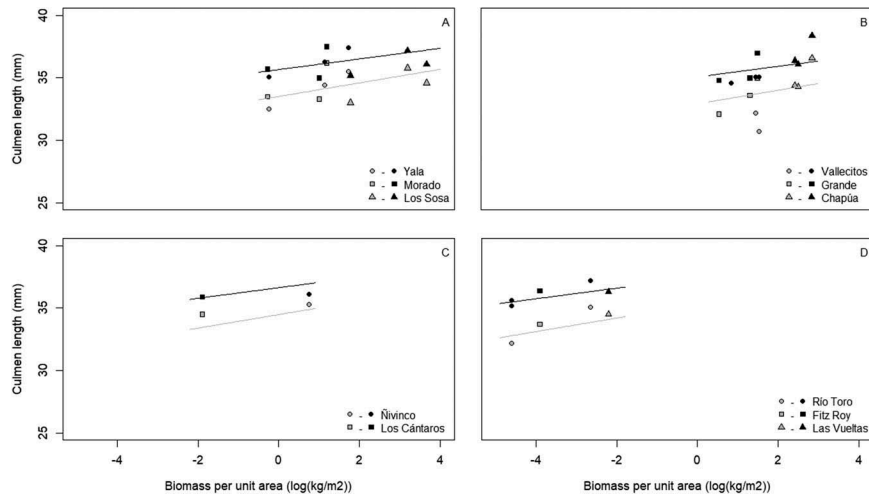
density (Schoener 1983; Adams 2001). In the Andean rivers of northern Argentina, Torrent Duck densities ranged from 1.7 to 4.2 ducks/km (Sardina Aragón *et al.* 2011) and from 0.7 to 3.5 ducks/km in the central-north region (Álvarez *et al.* 2014). Small populations have been recorded in the central-south region, but without density estimations (Cerón and Trejo 2012), and density was estimated at 0.5 ducks/km in the south region (Vila and Aprile 2005). The latitudinal increase in territory size can therefore be explained both by the steep decline in food availability and by the decrease in competitor densities. The river specialist Blue Duck from New Zealand can also markedly reduce territory size in response to increasing population densities (Williams 1991). However, to fully understand the possible regulatory mechanisms of intraspecific interactions on the territory size of anatids specialised in fast flooded rivers, variation in duck density and territory size should also be studied at the population level.

Our results showed that territory size was negatively and significantly related to food density. However, much of the variability in territory size and food





**Figure 5.** Variation in territory size in relation to culmen length of (A) female (territory size =  $9246.51 - 29.44 \times \text{female culmen}$ ); and (B) male (territory size =  $684.84 + 208.27 \times \text{male culmen}$ ) Torrent Ducks in the four sampling regions. See supplementary material S3 for parameter estimates.



**Figure 6.** Relationships between culmen length of male (black symbols) and female (grey symbols) Torrent Ducks and aquatic invertebrate biomass per unit area in four regions of the Argentinian Andes: (A) north; (B) central-north; (C) central-south; and (D) south regions. Different predicted lines with different intercepts for each region are shown. See supplementary material S3 for parameters estimates.

availability resided in random effects, i.e. in the natural structure of our study system (note the differences between marginal  $R^2$  and conditional  $R^2$ ; Nakagawa and Schielzeth 2013). For instance, food availability explained 38% of the total variance in territory size,

while the combined effects of food availability and the nested structure of rivers in the regions explained 75% of the total variance. The tendency to a more strongly negative relationship between food availability and territory size in the southern region than in the others

(Figure 4(A)) suggests that territory size is more strongly related to duck densities and food availability where food availability is limiting. The reasons that caused the slight differences in the relationship between food availability and territory size in the different regions (Figure 4(A)) require further studies including, for example, flood events. Flood events have a negative effect on Torrent Duck populations (Pernollet 2010), probably because they reduce invertebrate densities, as has been described for the Blue Duck (Veltman *et al.* 1991; Godfrey *et al.* 2003). Therefore, although territory size seems to be influenced by food availability and duck density, it could also be expected to be influenced by other characteristics of territory quality not evaluated in our study, such as the availability of shelters and nesting sites, and the stability of the territory when floods occur. The relative importance of these variables could be larger in areas less limited by food, such as the northern and central-north regions in the Argentinian Andes.

For habitat-specialist species, habitat availability may be a limiting resource which affects population size because competition for space may restrict the breeding population, favouring the most aggressive and/or larger birds (Brown 1964). High territoriality in the Torrent Duck supports the idea that territories are a valuable and scarce or limiting resource (Cerón 2012). Moreover, the best territories in terms of food availability are owned by the pairs of ducks with the largest body sizes. However, the spatial structure of territory quality highlights the importance of using empirical data across the species distribution range to assess models of bird territoriality. We suggest that the strong selective pressure imposed by a changing environment such as mountain rivers (Benistom 2003) may have led the Torrent Duck to develop territorial behaviour involving (i) year-round territoriality in both sexes (Eldridge 1986b), (ii) territory defence positively related to body size, and (iii) territory sizes that depend on food availability and population densities.

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