



PLUMAGE MATURATION, MOLT, AND MORPHOLOGY OF THE CRITICALLY ENDANGERED HOODED GREBE (*Podiceps gallardoi*)

Maduración del plumaje, muda y morfología del críticamente amenazado Macá Tobiano (*Podiceps gallardoi*)

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ABSTRACT: The understanding of morphological and behavioral aspects of bird species can guide appropriate management actions for their conservation. Grebes (Podicipedidae) are peculiar in their molting strategy, since body feathers are continuously replaced during the whole year. Available information about natural history of Neotropical grebes is scattered. The Hooded Grebe (*Podiceps gallardoi*) is a critically endangered species with a global population of less than 800 individuals that inhabits the remote highlands plateaus of Austral Patagonia. In this work we present information about sexual differences in molting behavior, plumage coloration and morphological characteristics of this species. During seven years we monitored the whole population of Hooded Grebe and collected data from field observations and from collected individuals that had been killed by American mink. Our results show sexual differences in morphology, and in timing of molting, but not in coloration in the UV and visible range. Hooded Grebe's molting strategy differs from that of other grebes, including closely related species, as it lacks molting migration and does not develop a visibly different alternate winter plumage. Molting strategies and morphological differences between sexes may represent adaptations to variable conditions in extreme environments of southern Patagonia.

KEYWORDS: conservation, Hooded Grebe, molt, molting migration, natural history, Patagonia, plumage, *Podiceps gallardoi*

RESUMEN: La comprensión de los aspectos morfológicos y de comportamiento de las aves puede guiar las acciones de manejo apropiadas para su conservación. Los macaes o zambullidores (Podicipedidae) son peculiares en su estrategia de muda, ya que las plumas de contorno se reemplazan de forma continua durante todo el año. La información disponible sobre la historia natural de los macaes neotropicales es escasa. El Macá Tobiano (*Podiceps gallardoi*) es una especie en peligro crítico con una población global de menos de 800 individuos que habita en las remotas mesetas de altura de la Patagonia Austral. En este trabajo presentamos información sobre las diferencias sexuales en el comportamiento de muda, la coloración del plumaje y las características morfológicas de esta especie. Durante siete años monitoreamos a toda la población del Macá Tobiano recopilando datos provenientes de observaciones de campo y de individuos colectados, muertos por visones americanos. Nuestros resultados muestran diferencias sexuales en morfología y en el momento de la muda, pero no en la coloración en el rango UV ni en el rango visible. La estrategia de muda de Macá Tobiano difiere de la de otros macaes, incluso de las especies estrechamente relacionadas, en la ausencia de migración de muda y de un plumaje invernal alternativo perceptible. Las estrategias de muda y las diferencias morfológicas entre sexos pueden representar adaptaciones a condiciones variables en los ambientes extremos de la Patagonia Austral.

PALABRAS CLAVE: conservación, historia natural, Macá Tobiano, migración de muda, muda, Patagonia, plumaje, *Podiceps gallardoi*

Understanding the natural history traits of a species is the first step toward a deeper comprehension of the complex patterns in its biology, and more importantly, this understanding can guide effective management actions for the conservation of threatened species (Sutherland 1998). Morphological, physiological and behavioral characteristics compose the very essence of a species. Molting is one example of these characteristics, since it is a highly energetic demanding event, common to all bird species, and represents a critical period in their life cycle (Humple et al. 2013). The high-energy cost of molting is assumed to be an impediment for most birds to molt and breed at the same time (Payne 1972).

Grebes (Podicipedidae) are a well-known group of birds (Konter 2001, Ogilvie 2003, Fjeldså 2004, Winkler et al. 2020). There are several studies on the morphological characteristics of grebes, but most of them focused on the evolutionary aspects (Mayr 2004), although there are some examples of morphological changes related to behavioral traits (i.e., Jehl 1997). Morphological studies on grebes have shown that ecological displacement in closely related species that occur together is an important evolutionary process, which involves the modification of behavioral and morphological characteristics (Fjeldså 1983).

From a conservation perspective, there are examples that highlight the importance of morphological characteristics in grebes. For instance, morphological traits have been used to compare data from Lake Atitlán and to distinguish the Pied-billed Grebe (*Podilymbus podiceps*) from the extinct, much larger Atitlán Grebe (*P. gigas*) (Hunter 1988). Moreover, other studies have focused on environmental pollution, and its potential effect on molting cycle or pigment deposition on grebes (Hartman et al. 2017, Pyle & McPherson 2017).

Grebes are particularly peculiar in their molting strategy. Body feathers are continuously replaced during the whole year, whereas flight feathers are shed synchronically, including remiges and some wing coverts (Fjeldså 2004, Pyle 2008). Species vary greatly in timing of the molting (Storer 1967), and some of them even migrate towards special molting areas (Pyle 2008). This behavior, called 'molt migration', occurs after the breeding period (Storer & Jehl 1985, Piersma & Van Eerden 1988, Stout & Cooke 2003, Humple et al. 2013), and individuals stay in sites with stable food supply and low predation risk (Fjeldså 2004, Humple et al. 2013). The usually high concentration of molting individuals in specific sites increases populations'

vulnerability to changes in food resources, weather, predator abundance, and contamination (Humple et al. 2013, Hartman et al. 2017), representing a critical stage in grebes' life history. Thus, understanding molting behavior is vital for grebes conservation in general and for threatened grebes in particular (Pyle et al. 2009).

Birds are sensitive to reflectance of low wavelengths (300-400 nm) (Osorio et al. 1999, Cuthill et al. 2000) and since the discovery of that, the study of avian plumage coloration has changed radically (Eaton 2005). Although intersexual differences of UV coloration in birds are very common (Eaton 2005), there are no published studies in grebes, despite most species of grebe are, at least to the human eye, non-dichromatic (Winkler et al. 2020).

Available information about natural history of Neotropical grebes is scattered, relatively old, and available only for a reduced group of species, particularly those that inhabit North America (Llimona & del Hoyo 1992, Winkler et al. 2020). The Hooded Grebe (*Podiceps gallardoi*) is an exception for this. The extreme rarity of this critically endangered species (Birdlife International 2024) and the fact that there are c. 400 breeding pairs scattered in one of the most remote landscapes of the world (Roesler 2012a) set a challenge to comprehensive, large scale and systematic studies. However, since the discovery -for occidental science- by Rumboll in 1974, several articles about its natural history, ecology and biology have been published (Lange 1981, Storer 1982, Erize 1983, Fjeldså 1986, Beltrán et al. 1992). Nevertheless, the information presented was based on non-systematic studies and came from restricted areas of the species' distribution. Few publications mentioned plumage characteristics (Rumboll 1974, Erize 1983), and only one article was exclusively about aspects of the plumage, focusing on chicks' downy plumage (Nuechterlein & Johnson 1981). Molting migration was suggested for the Hooded Grebe considering the similarity with other *Podiceps* species (Storer & Jehl 1985), but there have been no formal studies about molting of this species (Imberti et al. 2020).

The aim of this study is to present novel information about sexual differences in molting behavior, plumage coloration and morphological characteristics of the Hooded Grebe that may help to better understand life history traits of this critically endangered species and guide management actions for its conservation.

METHODS

Hooded Grebe reproduces exclusively in basaltic plateaus of southwestern Austral Patagonia, in Santa Cruz Province, southern Argentina (from 46°41'S to 50°35'S). We monitored reproductive lakes for seven consecutive breeding seasons (November–April) from 2008–2009 to 2014–2015 (field effort was 1041 man/days of direct observations). During fieldwork, we monitored banded and not banded individuals. Field observations were carried out since November, after the arrival of individuals to the breeding grounds, to early May, when most individuals migrate (Roesler 2016). During the non-breeding season (May–Oct) we monitored Hooded Grebe at least once per month at Cardiel Lake and the main estuaries of Santa Cruz Province (Santa Cruz, Coyle and Río Gallegos rivers; Roesler 2016). We detected three events of surplus killing by American mink (*Neogale vison*) twice at El Cervecerito Lake (Buenos Aires Lake Plateau – hereafter ‘BALP’) and once at C199 Lake (Siberia Plateau – hereafter ‘Siberia’) (further details in Roesler et al. 2012b, Fasola & Roesler 2018). All dead individuals we recovered within 18 h since they were killed. We weighted, measured, sexed, and evaluated for molting stage all collected individuals, only when possible since conditions of some birds were not suitable and therefore those individuals were discarded (i.e., head destroyed during the mink attacks). As the three surplus killing events happened while Hooded Grebe were breeding, we use ‘colony’ to name the different groups of grebes collected. We took the following morphological measurements: bill length, from the tip to start of the feathers, and tarsus length, both using a Vernier caliper (± 0.02 mm), and weight using a 1000 g Pesola spring balance ($\pm 0.3\%$). Sex was determined by direct observation of gonads. The stage of the colony, date of depredation, and number depredated (and collected) individuals were: Colony 1 at El Cervecerito Lake at BALP (nests with eggs), March 7, 2011, 8 females and 10 males; Colony 2 at C199 in Siberia Plateau (chicks of >3weeks of age), March 17, 2013, 4 females and 6 males; and Colony 3 at El Cervecerito Lake in BALP (chicks of >3weeks of age), March 5, 2013, 6 females and 10 males.

For each adult individual collected, we analyzed the molting stage by comparing the molt prevalence of flight feathers’ (growing remiges, old remiges still present and fully-grown new remiges). We obtained data from 12 adult females and 16 adult males collected in early-mid March (this subset of the total collected individuals was due to bad preservation of wing feathers of some individuals –we only used individuals in good condition–). To compare molting stages between sexes, we performed an exact 2x2 Fisher probability test, since more than 20% of the expected frequencies (molt/no molt) were equal to or less than five. Data on molt migration and juvenile molting was collected through field observations of live individuals during the breeding (+4500 person/days of field observation) and non-breeding seasons (+900 person/days of field observation).

We studied plumage coloration on two females and four males (deposited at La Plata Museum, University of La Plata), all collected at colony 3 (El Cervecerito on March 5th 2013). We measured plumage coloration in the 300–700 nm spectral range using an Ocean Optics® USB2000 reflectance spectrophotometer with illumination by a PX-2 pulsed xenon light, both connected to a bifurcated fiberoptic cable. The sensor was mounted in a probe with an inner diameter of 6 mm. We calibrated reflectance measurements using a standard white surface (barium sulphate; Osorio & Ham 2002) and a black standard (light source off). We saved reflectance spectra through *Spectra suite* software taking reflectance values at intervals of 0.35 nm. We measured reflectance for four body regions: forehead, crown, breast and underbelly and for each body part we calculated an average of three measurements. We did not include forehead and crown measurements in the analysis since they were affected by the conditions of the specimens (presence of blood on the plumage). For the two remaining plumage regions, we analyzed sexual differences in brightness and chroma. Total brightness values were calculated as the sum of reflectance (R) across all wavelengths ($\Sigma R_{300-700}$) and UV, blue, green and red chroma were calculated as follows: UV chroma = $\Sigma R_{300-399} / \Sigma R_{300-700}$, blue chroma = $\Sigma R_{400-499} / \Sigma R_{300-700}$, green chroma = $\Sigma R_{500-599} / \Sigma R_{300-700}$, and red chroma = $\Sigma R_{600-700} / \Sigma R_{300-700}$.

To study individual condition along the breeding cycle we compared body mass at different stages in colonies at BALP (colony 1 at nesting stage vs. colony 3 at chick stage). We conducted a second analysis to compare body mass between individuals at a similar breeding stage but in different lakes within the same breeding season (March 2013), corresponding to individuals of colony 2 at Siberia and colony 3 at BALP. We analyzed sexual differences in exposed bill length using measurements of 8 females and 10 males from BALP, and all 4 females and 6 males from Siberia while we compared sexual differences in tarsal length using

measurements of 6 females and 10 males from BALP. We used non-parametric Mann-Whitney tests to compare body size differences between sexes. All analyzes were performed in R 3.2.2 (R Core Team 2015).

RESULTS

There were sexual differences in the stages of molting of flight feathers (remiges) by the end of the breeding season (March 2013). Only 2 of 12 females (16%) were molting in March, both at the final stage of molting (almost fully-grown flight feather), with the remaining 10 females with fully-grown feathers (molting finalized) (Fig. 1A). On the other hand, 9 of 16 males (56%) were still molting at the same period, all of them at an early stage of flight feather development ($P = 0.03$) (Fig. 1B).

As regard the development of adult plumage, field observations indicate that the Hooded Grebe attains its definitive plumage appearance throughout a gradual process that takes approximately seven months (data obtained based on +200 person/days of observation in non-breeding season between 2011-2018 – see Roesler 2016 for more effort details). After hatching, a soft and not very dense grayish downy plumage covers

the chicks, with lighter coloration in the ventral part and dark lines on the back and head (Fig. 2a). After the first week, coloration becomes more uniform, and head- and back's dark lines gradually disappear (Fig. 2b). When flight feathers and wing-coverts appear, its overall coloration seems bicolor, with ventral areas grayish-white, including neck and throat, and the entire dorsal parts, including the back, back of the neck and the entire head, dark plumbeous-gray, although some parts, such as the head, are almost black (Fig. 2c). Four-week-old chicks lose the down and feathers cover most of their bodies. The main feature of this plumage is the clear patch on the forehead (Fig. 2d). Thereafter, they do not change much in appearance until they acquire the definitive adult aspect. However, changes during this period (first basic/juvenile plumage) are more conspicuous in naked areas. The chick's iris coloration is dark (blackish), whereas in individuals over five months, iris coloration is dark reddish and the eye-ring yellowish, less bright than in adults. The pre-formative molt of the head (e.g., crest feathers and dark feathers on the throat) and the body results in a very similar appearance to that of adults (Fig. 2e). An auxiliary pre-formative molt may occur immediately afterwards and a partial pre-alternate molt seems to occur in late winter (Fig. 2f), making



Figure 1. Wing feathers molting stages. A) fully molted female (fresh feathers); B) early molting on male. Both individuals collected at El Cervecero Lake, Buenos Aires Lake Plateau, in March 2011 (Photos: I. Roesler).

Table 1. Reflectance values obtained from females ($N = 2$) and males ($N = 4$). Chest 1: mean value of upper part of the breast; chest 2: mean value of the lower part of the breast; belly: mean value of belly area.

	Females			Males		
	Chest 1	Chest 2	Belly	Chest 1	Chest 2	Belly
Bright	5948.6	5412.6	4887.5	5500.5	5305.7	4633.1
Croma UV	0.146	0.164	0.172	0.147	0.144	0,151
Croma Azul	0.240	0.248	0.252	0.249	0.243	0,248
Croma Verde	0.297	0.287	0.283	0.295	0.297	0,292
Croma Rojo	0.315	0.298	0.291	0.307	0.314	0,306

Table 2. Morphometric variables of individuals collected at El Cervecer Lake (BALP) and C199 Lake (Siberia) grouped by sex.

	n	Mean	SD	Median	Min.	Max.
Weight Female	18	527.5	54.4	542,5	400	600
Weight Male	26	571.8	142.8	610	625	780
Tarsi Female	8	47.2	1.1	47.4	45.1	48.6
TarsiMale	10	48.8	1.8	48.8	46.3	51.4
Culmen Female	12	19.0	2.1	19.0	16.3	23.0
Culmen Male	16	21.0	1	21.3	17.1	23.7

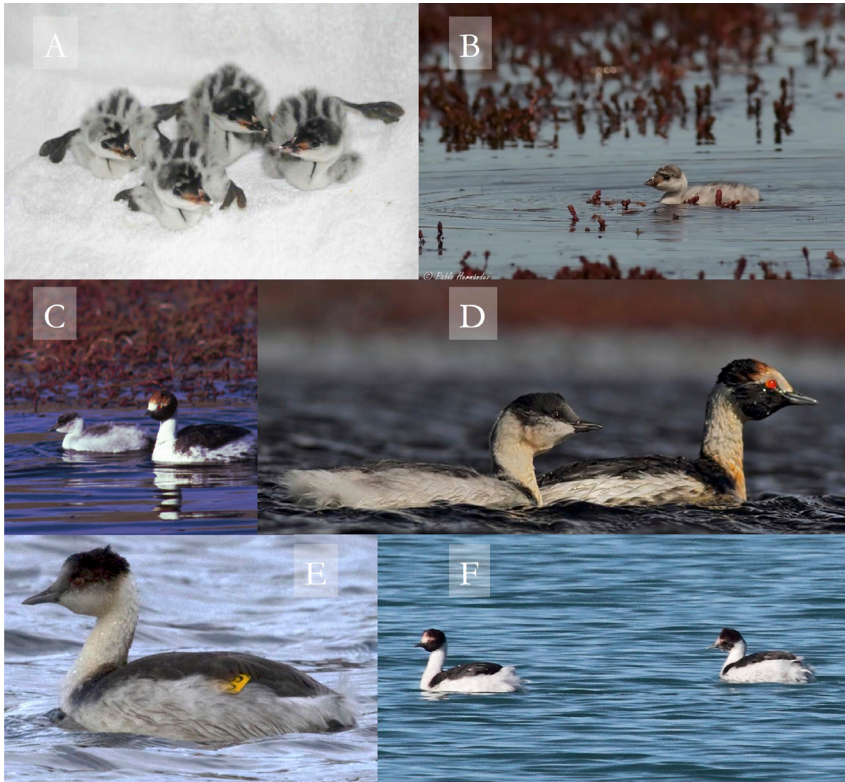


Figure 2. Hooded Grebe's molting process sequence: downy chick to definitive plumage. Individuals age: A) 1–2 days old (Photo: Proyecto Macá Tobiano/Aves Argentinas); B) c. 10 days-old (Photo: P. Hernández); C) 20–30 days-old (left individual parental adult) (Photo: M. Thibaud); D) 30–40 days-old (with the parental adult) (Photo: P. Hernández); E) c. 4 month-old (Photo: S. Imberti); F) c. 6 month-old (Photo: S. Imberti).

first cycle birds look indistinguishable from older adults.

We did not find sexual dichromatism in chest and belly (Table 1). However, we found significant differences between sexes in morphology (Table 2). Males had a longer bill (exposed culmen) than females ($w = 38.5$, $P < 0.007$) and a tendency of longer tarsi ($w = 19$; $P = 0.06$). Body mass of males was also higher than that of females ($w = 92.5$, $P = 0.0007$). We found differences in body mass between individuals of BALP colonies ($w = 232.5$, $P = 0.002$). Individuals from colony 1 (females mean weight = 556.7 g; males mean weight = 604 g) were heavier than those of colony 3 (females mean weight = 490 g; males mean weight = 538 g). Also, we detected differences between individuals from the colony 3 of BALP and colony 2 of Siberia ($w = 130.5$, $P = 0.008$), with heavier individuals in colony 2 (females mean weight = 521.2 g; males mean weight = 677.5 g).

DISCUSSION

The data presented here suggest that molting of Hooded Grebe's wing feathers occurs while breeding. Only in the Pied-billed Grebe (*Podilymbus podiceps*), definitive prebasic molt has been mentioned to occur during the breeding period, even while incubating (Pyle 2008), but it was detected to happen at a very low frequency (only in one out of 27 examined individuals, Otto 1985). Also, our data suggest that timing of molting differs between Hooded Grebe's sexes, with females molting earlier than males. In Great-crested Grebe (*Podiceps cristatus*) males and females also show slightly different molt peaks, although they overlap widely during the molting process (Piersma 1988).

Field observations of Hooded Grebe indicate that molting of females (primary feathers) begins in late January, whereas in males this happens around mid-February (see Roesler 2016 for more details on field effort). Explanation of this sexual difference could be related to sexual differences in other behaviors (i.e., incubation and chick care or migration) but available data do not indicate sexual differences in parental care or in migration behavior (Roesler 2016). Another potential explanation for differences in timing of molting could be the sexual differences in body mass, but there are other grebes species that differ in body mass and do not differ in timing of molting (Fjeldså 2004).

In most grebe species, the molting of contour feathers occurs continuously throughout the year,

which has been explained as an adaptation to maintain the waterproof condition of their plumage, and in contrast, the molting of wing feathers occurs synchronously (Fjeldså 2004, Pyle 2008, Howell 2010). Hooded Grebe shares the same molting pattern than the rest of grebes, but the timing of molt of wing-feather is not consistent with the migration molt mentioned for this species (J. Fjeldså in R. W. Storer & Jehl 1985). There are several hypotheses to explain molt migration in other grebe species, which are not mutually excluding. Most hypotheses focus on migration to ecologically stable sites or to sites with low predation risk, like bigger lakes and/or the ocean (Stout & Cooke 2003). Another plausible explanation could be to avoid competition for food with non-flying juveniles. If those explanations are accurate, Hooded Grebe's habitat seems fulfill the needs (i.e., habitats with low predation risk, enough stability, and no resources competition with juveniles).

The timing of molt in most grebe species is likely related to the need for adults to maintain their feathers in good condition while caring for chicks before the autumn migration, when the post-breeding molt typically occurs (Stout & Cooke 2003). The exceptionally early "breeding molt" (simultaneous molt of flight feathers) observed in the Hooded Grebe has been described in another species, the Pied-billed Grebe (Otto 1985), but only as an exception in a single colony, rather than what seems to be a consistent pattern as proposed by our data in the Hooded Grebe. Unlike other species, the Hooded Grebe's wing molt seems to be synchronized with nesting and includes the chick-rearing period. The high food quality of the Hooded Grebe's breeding lakes, along with adequate food availability, appears sufficient to avoid competition with juveniles—a factor often cited as a reason for the molting migration in other grebe species. Another key characteristic of Hooded Grebe's breeding lakes is the natural absence of native aquatic predators, combined with their size, which helps deter native terrestrial predators. The Hooded Grebe's pre-migratory molt may also be explained by the historical instability of its wintering grounds, which were impacted by glacial activity affecting river estuaries and large lowland lakes (Gilli et al. 2001). Most grebes have bright plumage during the breeding season (alternate plumage) and a dull visually different plumage in winter-time (basic plumage) (Pyle 2008, Howell 2010). On the contrary, some species of the Southern Hemisphere remain similar in their overall plumage throughout the year, as is the case of the Silvery Grebe (*P. occipitalis*), in which the basic plumage is just slightly opaquer

but somehow alike to the breeding (alternate) plumage (Fjelds  2004). Hooded Grebe differs from most species of Podicipedidae, and especially from other *Podiceps* species, showing the overall same plumage aspects throughout the year with no noticeable changes in its coloration or brightness (at least for the human eye both in the field and museum individuals).

Plumage of the recently hatched Hooded Grebe's chicks was described in the past (Nuechterlein & Johnson 1981) mentioning that they were similar to most grebes' chicks, but with more uniform coloration. They mentioned one important difference: Lack of the naked patch in the crown, present in all other chicks. Fjelds  (2004) described that the lined pattern disappears quickly, and his observation is concordant with ours. Two-week-old chicks' coloration is uniform and gradually begins to darken up until reaching juvenile plumage. Molting process to definitive plumage in first cycle birds needs to be studied more deeply, although information gathered during our studies suggests that it occurs during the central winter months (June-July). Fjelds  (2004) mentioned that first year individuals could have white feathers on their faces and napes. This pattern was however not observed in a one-year-old banded individual observed at a breeding site, that looks visually alike to an older adult (Roesler ump. data).

No color differences were detected between sexes in chest and underbelly plumage. Accordingly, no sexual differences in coloration have been described in any other grebe species (Fjelds  2004), although these studies did not use reflectance spectrophotometry to objectively assess plumage color. We should however point out that unmeasured plumage regions might -or not- be dichromatic. The crown, for example, is quite important during reproductive courtships (Storer 1982), but unfortunately measurements on head feathers were not possible due to the bad condition of collected individuals.

We found that males were heavier and had a longer bill than females. Size differences between sexes in the Hooded Grebe had been also mentioned in the past (Straneck & Johnson 1984). Our study described the extent of sexual dimorphism in body mass and in bill length, which could be used as a tool for sex identification in behavioral field studies, with a reliable degree of certainty, as mentioned for Eared Grebe (*P. nigricollis*) (S  ez-G  mez et al. 2017). Although bill dimorphism is probably a consequence of allometry, it could have a great importance from an ecological perspective, as it would be possible the existence of sexual

ecological displacement in Hooded Grebe. Ecological displacement in grebes has been described when two sympatric species of the same genus occur together, including Hooded and Silvery Grebe in the highland lakes of Santa Cruz Province (Fjelds  1983). Bill differences among sexes may generate that sexes forage differently, taking advantages of different resources.

An interesting finding was the differences in body mass in individuals from different colonies. Individuals of the colony 1 at BALP, which were in incubation period, were significantly heavier than individuals of the same lake that had 4-week-old chicks. The loss of body mass of nearly 12%, both in males and females, was possibly a consequence of the parental care of chicks. However, we cannot definitively rule out an effect of the year (data correspond to different breeding seasons). It is striking that adults collected in Siberia Plateau that were at "chick stages" of the breeding cycle (four-week-old chicks) had a similar weight to those nesting individuals (incubation stage) from BALP. A potential explanation is that food items available at each lake are different. The Siberia Plateau's lakes are rich in amphipods while snails are poorly represented, meanwhile the opposite situation occurs at BALP's lakes (Adami 2016, J. Lancelotti & I. Roesler in prep.). Amphipods seem to have a primary role as food source in Hooded Grebe's lakes (Lancelotti et al. 2015). A comparative studies of the diet and growth of exotic Rainbow Trout (*Oncorhynchus mykiss*) at Stobel Lake Plateau (within Hooded Grebe breeding distribution) indicate that the condition and growth of trout are strongly affected by the abundance of amphipods in their diet (Lancelotti et al. 2016). However, these results need to be evaluated in a more comprehensive study, since data was collected in different years, which could influence body condition due to other factors, such as climatic conditions.

Our results suggest that the Hooded Grebe differs in many aspects from most grebe species, even closely related ones, especially on molting strategies and timing. Molting strategies and morphological differences between sexes may represent adaptations to the variable conditions in the extreme environments of southern Patagonia. These results highlight the importance of management actions that have been undertaken (Roesler et al. 2016). Mostly those related to adult protection such as 'colony guardian' strategy during breeding (Roesler et al. 2016) and mink management, since during this period of their cycle adult grebes have no strategies to avoid alien invasive species, such as the American mink (Fasola & Roesler 2018).

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