Ecology and Conservation of the Titicaca Grebe (*Rollandia microptera*)



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Doctor of Philosophy



Declaration

I declare that this thesis has been composed by myself, and the work contained herein is my own, except when mentioned in the text. The work contained herein has not been submitted as part of any other degree or qualification.



Daniel A. Villar

December 16, 2024

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It is not possible to do science in indigenous areas without the collaboration of the people who live there. I would like to thank all of the local people of all the villages in Peru and Bolivia who so kindly let me into their communities, and allowed me to do this work. There are too many to thank individually, but I especially would like to thank Eloy, for being on the most boat trips with me out of Piata, and Doña Juana for arranging my contacts with Uro fishers and hunters.

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Publications and Contributions

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Abstract

The Titicaca Grebe is an endemic endangered species found in Lake Titicaca and outlying waters in the Altiplano region of Peru and Bolivia. It faces myriad threats, from climate change to fisheries bycatch, but suffers from a lack of even basic information on its natural history and ecology, such as its population and feeding habits. This thesis has been an attempt to remedy this deficiency in natural history knowledge, and in placing the Titicaca Grebe within its broader social-ecological context. I found that the population of the Titicaca Grebe is almost certainly greater than had been assumed previously by the International Union of the Conservation of Nature, which had been relying on a population census conducted in 2003. However, I also found that the Titicaca Grebe is suffering from high rates of fisheries bycatch, though the exact rate of bycatch remains difficult to establish. I also investigated conflict between the Titicaca Grebe and local indigenous Aymara, Quechua, and Uru people, especially as it relates to fisheries. I found that while most people are apathetic about the Titicaca Grebe, the hostility towards it from fishermen, occasioned by its perception as being in competition for fish, is a major barrier for its conservation. I attempted to address this conflict through studying the diet of the Titicaca Grebe, and by studying how economic change in the Lake Titicaca region influences how local people manage natural resources, such as the totora sedge, and what downstream effects that has on the Titicaca Grebe.

1

Introduction

Theoretical Background: Ethnobiology and Ethnoecology

While the ideal of "wilderness" as being an area free of human impact remains influential in popular conceptions of conservation, there is no ecosystem which is entirely free of anthropogenic disturbance, including wilderness areas which are the focus of much global conservation work (Watson et al. 2016). In most popular understandings of conservation, human modified systems have been considered to be diametrically opposed to natural ones, with the former being unworthy of being preserved (Lorimer, 2015; Young & Duchicela, 2020). However, there is a rich global literature on the role of cultural practices in maintaining biodiversity, and how changing cultural practices for "less" human imprint can, paradoxically, harm some species. The prototypical examples of work on such cultural landscapes have tended to be in agricultural landscapes, Oliver Rackham's work on English woodlands and the English countryside (Rackham, 1986), T. C. Smout's work on Scottish agricultural biodiversity and changing agricultural practices (Smout, 2000), and William Cronon's work on biodiversity in New England following English conquest (Cronon, 1983).

Like much of Europe where the first studies of cultural landscapes occurred, the central Andes is a landscape with millennia of history of intense modification of the landscape (Ellenberg, 1979; Erickson, 2000). The very name "Andes" refers to the terraces, known in Spanish as *andenes*, which can still be found on almost every mountainside in the Central Andean region (Ellenberg, 1979). Because of this, the Andes has been a hotspot for ethnoecological research and research into non-western cultural landscapes (Ibarra et al., 2023; Sarmiento, 2000, 2005, 2010). Much of this work has occurred under the umbrella of montology, a transdisciplinary science of mountain landscapes which incorporates methodologies and insights from ecology, biogeography, anthropology, and geography to understand mountain landscapes (Sarmiento,

2020). In the Andean context, this has included work on how historic cultural practices influence the distribution of birds and plants across the Andean region (Sarmiento, 2010), and how Andean cosmovision influences conservation efforts (Ibarra et al., 2023). Key to this montological and ethnoecological research paradigm is the integration of indigenous perspectives into research (Sarmiento, 2005; Ibarra et al. 2023)

Key to ethnoecology is understanding what makes each species and locale unique. All ecology is, to a certain extent, the science of the particular rather than science of the universal — while there are universal laws, especially at the level of mechanism, most aspects of ecology rely on both historic and situational contingency. In this thesis, Lake Titicaca is the specific place of study, the Titicaca Grebe the specific species of study, and the Aymara, Quechua, and Uru people who fish on Lake Titicaca the cultural background of the study region (Fig. 1). In this thesis, I have focused on how economics changes the cultural practices of the people of Lake Titicaca, and how this impacts the Titicaca Grebe, with an emphasis on the conservation implications of my ethnoecological research findings.

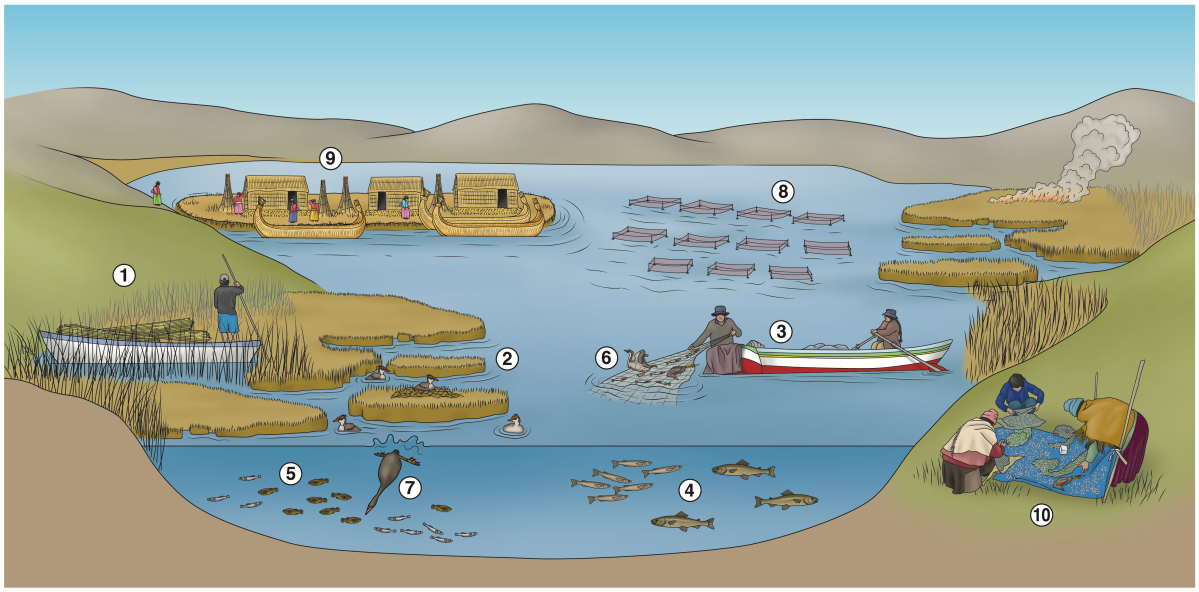


Figure 1 A simplified graphical representation of Lake Titicaca and its ethnoecology, including several interactions which are the focus of this thesis. 1) traditional harvesting of totora (Schoenoplectus californicus subp. tatora) 2) Titicaca Grebe nesting in totora wetland 3) subsistence fishing in Lake Titicaca 4) Invasive pejerrey (Odontesthes bonariensis) and salmonids in the lake 5) native Orestias sp. fish 6) Titicaca Grebes being caught as fisheries bycatch 7) A Grebe hunting for native species 8) fish farming in the lake 9) Uru floating islands used for tourism 10) shoreside processing of fisheries catch. Image Credit: Debbie Maizels.

Ethnobiology and Conservation

Ethnobiology is a discipline at the crossroads between anthropology and biology, and focuses on how humans and nature interact, while also questioning the dichotomy between the two. It attempts to incorporate both the self-reflective and understanding of the importance of the subjective of anthropology, with the objective rigour of ecology (Anderson, 2011). Central to ethnobiology is the study of Traditional Ecological Knowledge (TEK). TEK is the knowledge of a natural environment which a people build up over generations through living in that environment (Huntington, 2000). TEK is sometimes contrasted with Local Ecological Knowledge (LEK), which is knowledge local people hold about their environment that is not vertically transmitted (Aswani et al., 2018). While both terms are used in different chapters, I make no significant distinction between the two for the purposes of this thesis.

Within ethnobiology, ethno-ornithology is a relatively nascent sub-discipline. While there were early accounts of how indigenous people viewed birds and understood birds amongst the naturalist accounts which form the pre-history of ethnobiology (Stresemann, 1975; Vuilleumier, 2003), I am only aware of two uses of the term ethno-ornithology before the 1970s (Speck, 1946; Schaeffer, 1950), though of course the study of folk biology, including some of what we would today call ethno-ornithology, did exist (Diamond, 1966; Berlin et al., 1966). From the 1970s, more ornithologists became interested in ethnography, and ethnographers interested in human-bird relations, leading to the beginnings of ornithology as we understand it today (Majnep & Bulmer, 1977). Since the turn of the present century, interest in ethno-ornithology has increased, as has interest in the intersection between social science and ornithology more generally (Tidemann & Gosler, 2010; Dayer et al., 2020). This has been reflected in the growth of books and papers specifically dedicated to the role of birds in human culture, both in the academic press (Tidemann & Gosler, 2010; Cocker & Tipling, 2013; Gardella & Krute, 2024), and in the popular press (Birkhead, 2022; Moss, 2024). Many ornithologists have also shown an increased willingness to recognise the importance of integrating non-western perspectives into the mainstream of ornithology and biology more broadly (Huntington, 2000; Molnár & Babai, 2021; Thomsen et al., 2024), especially amongst those working in conservation biology (Gilchrist et al., 2005; Ramos, 2018; Dayer et al., 2020).

Historically, most conservation was done either in opposition to local people, or against the wishes and interests of local people (Dowie, 2009; Sarkar & Montoya, 2011). This "fortress conservation" relied on the complete extrication of local people from nature in order to protect it (Redford & Sanderson, 2000; Sarkar & Montoya, 2011), completely ignoring both the rights of local people, and oblivious of their role through traditional ecological practices in promoting biodiversity. For decades, the fortress conservation model has had critics, both from indigenous

rights activists and from those who argued that it is both unethical and counter-productive to the interests of conservation in the long-run (Orlove, 1991; Burnham, 2000). Today, widespread acknowledgement exists of the importance of working with local people in conservation, and of incorporating their needs and perspectives into conservation and wildlife management decision making (Drew & Henne, 2006; Sarkar & Montoya, 2011; Reyes-García & Benyei, 2019; Ibarra et al., 2023; Mahalwal & Kabra, 2023).

Being at the crossroads of ecology and anthropology, ethnobiology is perfectly placed as a discipline to facilitate the integration of TEK into conservation (Huntington, 2000; Alves, 2013; Wolverton et al., 2023). Its potential contributions are diverse. TEK can, for example, inform conservationists about the past abundance of species which have not been monitored (Anadón et al., 2009; Veneroni & Fernandez, 2021), provide information about seasonal animal movements (Huntington et al., 2004), can provide information on the traditional uses of a landscape which might promote biodiversity (Lake et al., 2017), of interactions between plants and animals of which ecologists are unaware (Nabhan, 2000), and provide information on the natural history of species which had not previously been well studied (Moller et al., 2004). Ethnobiology also allows conservationists to understand the social context of conservation efforts, including cultural attitudes which can shape conservation outcomes (Bennett, 2016; Sarmiento & Hitchner, 2017).

The Lake Titicaca Ecosystem

Geographic Location and Geologic History

Lake Titicaca is a high-altitude freshwater lake with a surface altitude of roughly 3,810 metres (Wirrmann, 1992), though the exact surface level fluctuates by year and season. Lake Titicaca is embedded in the heart of the Altiplano, a large flat plateau in the central Andes shared between Peru and Bolivia. The region around Lake Titicaca is puna grassland (Dinerstein et al., 1995). The lake is endorheic, and forms the terminus of a watershed that is independent of both the Atlantic and the Pacific (Roche et al., 1992). Only evaporation, and the Desaguadero River, which used to connect it to Lake Poopó before that lake's drying up because of climate change (Perreault, 2020), prevents continual water level rising.

Lake Titicaca is the latest of five paleolakes that have existed on this site since the Late Pliocene/Early Pleistocene (Lavenú, 1992; Fornari et al., 2001; Placzek et al., 2006; Fritz et al., 2007; Placzek et al., 2013), each characterised by a contraction or expansion of water levels, rather than being entirely new lakes after a complete drying of the region. The oldest of these paleolakes is Lake Mataro, which existed as early as 2.8 million years ago (MYA) (Fornari et al., 2001). Lake Mataro had a surface altitude of 3950 metres, or roughly 140 metres higher than the present lake surface. Lower lake levels 1.1MYA led to the formation of Lake Cabana, which had a surface altitude of 3900m, or 90 metres above the present lake level (Wirrmann & Mourguiart, 1995; Fornari et al., 2001). The next oldest paleolake is Lake Ballivián, which formed 600 thousand years ago (KYA) (Servant-Vildary, 1993). Lake Ballivián had a surface altitude of 3860m. It is during this period that tectonic shifts created the greatest depths of present Lake Titicaca (Lavenú, 1992). Traditionally, the fourth paleolake of Lake Titicaca was referred to as Lake Minchin, and existed 70-30 KYA (Lavenú, 1992; Fornari et al., 1992), with a lake surface of 3825 metres. However, some authors have questioned the existence of Lake Minchin, and instead suggest it is a series of smaller lakes which were not connected (Placzek et al., 2006). The latest of the paleolakes was Northern Lake Tauca (Blard et al., 2013), so

named to distinguish it from the larger Southern Lake Tauca that existed 18.5 – 14 KYA at the same time in what is now the Salar de Uyuni (Martin et al., 2018).

Within the Holocene, lake levels have fluctuated by several hundred metres (Guédron et al., 2023), while records in the 20th century indicate variation in lake level of several metres (Ronchail et al., 2014). In addition to these annual changes of lake level, seasonal fluctuations occur between the dry and wet seasons.

Vegetative Zones

The earliest attempt by western scientists to classify the vegetation of Lake Titicaca was by Tom Tutin, part of the 1937 Percy Sladen Expedition to Lake Titicaca. He classified Lake Titicaca into four major vegetative zones, named after the most common plants of each. In descending depth order, these are the *Zanichella-Potamegaton* Association, the *Myriphyllum-Elodea* Association, the *Chara* Association, and the *Sciaromium* Association (Tutin, 1940). He noted the existence of Totora (*Schoenoplectus californicus* subsp. *tatora*) (C.A. Mey.) Soják), but didn't consider it a significant vegetative zone of the lake because it was limited to sheltered bays, and appeared to be reliant on human cultivation.

This classification was revised in the late 20th century (Raynal-Roques et al., 1992), and is the primary classification used in this thesis, as it better reflects the current distribution of vegetative communities in Lake Titicaca. This system classifies the lake into three vegetative zones; totora wetland, llacho, and chara. Totora wetlands are characterised by totora, a sedge. It occurs primarily in shallow areas, between 1 and 4 metres in depth. Given totora's long history of human use and planting (Paduano et al., 2003; Bruno et al., 2021), it is likely that its

distribution is as much due to anthropogenic factors as abiotic ones. Despite its relatively recent arrival, the totora acts as an important habitat for many of the species of Lake Titicaca, including the Titicaca Grebe (*Rollandia microptera*) (Pulido Capurro, 2018). It also acts as a shelter for spawning fish, especially *Orestias* sp. (Vaux et al., 1988; Lauzanne, 1992; Vila et al., 2007), and is home to a variety of invertebrates (Vellard & Dejoux, 1992).

Llacho is characterised by milfoils and other soft aquatic plants, especially *Myriophyllum* sp. and *Elodea* sp. The Llacho vegetative zone can overlap in depth with the totora vegetative zone, especially in shallow parts of Lago Menor far from the shore. However, in general, llacho is found in slightly deeper waters to totora, between 3 and 9 metres in depth (Iltis & Mourguiart, 1992). Chara vegetation is characterised by fibrous stoneworts, such as *Chara* sp., and occurs at depths too deep for llacho or totora, between 9 and 12 metres in depth (Guerlesquin, 1992). No vegetation is found in Lake Titicaca beyond 12 metres depth.

Zoological Diversity

The most comprehensive survey of the entire biota of Lake Titicaca estimated that the lake harbours 533 species, of which 64 are endemic (Dejoux, 1994). However, this is an underestimate. New species have been discovered in Lake Titicaca since that survey (González & Coleman, 2002; González & Watling, 2003; Jaume et al., 2021), and undiscovered species are likely in the lake, especially amongst its invertebrates.

Lake Titicaca is one of the major centres of ichthyological endemism in South America, with 92% of native fish species being endemic (Albert et al., 2011). All native fish species in Lake Titicaca fall into two genera; *Orestias* and *Trichomycterus* (Lauzanne, 1992; Vila et al.,

2007). The latter genus includes two species of pencil catfish, *T. rivulatus* and *T. dispar*, neither of which is endemic to Lake Titicaca. Authorities differ in the numbers of species in the genus *Orestias* in Lake Titicaca, ranging from five (Villwock, 1986) to over 30 (Cruz-Jofré et al., 2013), but the most recent taxonomic revision of the genus in Lake Titicaca recognises 23 species (Takahashi & Moreno, 2015). Several *Orestias* species comprise related species complexes, such as the *Orestias cuvieri* complex and the *Orestias agasii* complex. Authors disagree on how many species complexes exist, and how best to delineate them (Parenti, 1984; Lüssen et al., 2003; Cruz-Jofré et al., 2013; Takahashi & Moreno, 2015). Five *Orestias* species have not been seen since the 1937 Percy Slade Expedition to Lake Titicaca, and are likely extinct (Northcote, 2000), including the largest endemic *Orestias* species, *Orestias cuvieri*.

In addition to these endemic species, two invasive fish species live in Lake Titicaca: rainbow trout (*Oncorhynchus mykiss*) and pejerrey (*Odonesthes bonariensis*) (Loubens & Osorio, 1992). Both were introduced in the 20th century, and both are of significant commercial importance to the lake's economy. Ecologically, both are predators, and have wreaked havoc on the Lake Titicaca ecosystem. The extinction of the Titicaca Orestias has been linked to these invasives, which have altered the invertebrate and plankton community of the lake (Vila et al., 2007; Anderson & Maldonado-Ocampo, 2011) with unknown consequences. In the open water of the middle of Lake Titicaca, far from vegetation, trout and pejerrey are often the only fish species found in abundance by fishers.

The most systematic survey of birds of Lake Titicaca published to date records 135 species (Pulido Capurro, 2018), including vagrants and seasonal migrants. The most common species in Lake Titicaca are the Andean Coot (*Fulica ardesiaca*) and the Andean Gull (*Chroicoceph-*

alus serranus). The latter is especially common near human settlements and in cities. A number of common duck species, such as the Andean Ruddyduck (*Oxyura ferruginea*) and the Puna Teal (*Spatula puna*) are also present, but Lake Titicaca is famed for its abundance of grebes, including the endemic Titicaca Grebe (*Rollandia microptera*). Almost all species congregate in the littoral, although Andean Gulls sometimes follow fishing vessels to the centre of Lake Titicaca in search of trout. Avian diversity is highest in the jungle of totora of Puno Bay, and in the mouth of the Ramis River (see map on page 99). Both provide ample breeding space for a variety of species, and the thick totora offers a modicum of protection from human hunters.

The majority of amphibians of Lake Titicaca are species common across the Andes, such as the Andean Frog (*Rhinella spinulosa*), or various species of four-eyed frog, such as the Juliaca Four-eyed Frog (*Pleurodema cinereum*). At least three fully aquatic amphibian species live in the lake, both of the genus *Telmatobius* – the Giant Frog (*Telmatobius gigas*), the Marbled Frog (*T. marmoratus*), and the Titicaca Water Frog (*T. culeus*). The last of these is endemic to Lake Titicaca. Most of the aquatic species in Lake Titicaca are restricted to the littoral, and are not found in waters of more than 5 m depth (Dejoux, 1992). However the Titicaca Water Frog has been recorded at over 100 metres depth (Cousteau & Landsburg, 1969), a record for any aquatic amphibian species. Like the Titicaca Grebe, the Titicaca Water Frog is at risk from fisheries bycatch and pollution (Angulo, 2008; Muñoz Saravia, 2018). It is also thought to be predated upon by invasive trout (Martín-Torrijos et al., 2016).

The invertebrate zoology of Lake Titicaca is poorly understood. New species are still often discovered in the region (Delgado & Ruiz-Tapiador, 2020; Jaume et al., 2021), and further studies are needed to further understand the diversity of invertebrates, and their role in the

ecology of the lake. Even relatively common groups of invertebrates, such as gastropods, have not been subject to systematic reviews for decades (Blume, 1958). Given how frequently new invertebrate species are found in Lake Titicaca, and the advances in systematics and genetic taxonomy since many of these reviews were published, it is likely that many invertebrate species await discovery in Lake Titicaca.

The Lake Titicaca Political Setting

Lake Titicaca is divided between Peru and Bolivia. To coordinate between them, the Autoridad Binacional Autónoma del Sistema Hídrico del Lago Titicaca, Río Desaguadero, Lago Poopó, Salar de Coipasa, better known as the ALT, was founded in 1996 (ALT, 2024). This organisation is primarily concerned with the economic utility of Lake Titicaca, through programmes of supporting fisheries in the lake by restocking native species (ALT 2023a), and coordinating water usage between the two countries (ALT 2023b). While the ALT does biodiversity conservation, it does not have a programme specifically dedicated for the Titicaca Grebe. In both countries, there exists environmental legislation which regulates fishing in Lake Titicaca. In Peru, this includes regulation on minimum catch size and periods when fishing is illegal (Ministerio de Producción, 2019a; Ministerio de Producción, 2019b). Unfortunately, these laws are often flaunted. While there are signs advertising the law's existence in the Puno offices of the Ministry of Production, which is the ministry in charge of fisheries in Peru, I could not find any fishermen who obeyed these laws. This is typical of many legalistic conservation interventions in regions where state capacity is not strong (Rose, 2011); legislation passed in the capital does not translate to action in the provinces, making it the conservation law equivalent of "paper parks" (Rife et al. 2013).

The only protected area in Lake Titicaca is the Reserva Nacional del Titicaca. Established in 1978, the Reserva and its regulations on fisheries and totora use have been a frequent source of conflict between conservationists and local people, especially Urus, since its foundation (Levieil & Orlove, 1990; Orlove, 1991; Orlove, 1993; Kent, 2008). Since 2005 the Peruvian government has recognised the ancestral rights of indigenous people to use traditional resources in protected areas – a law which was enacted largely as a response to conflict between Urus and the Reserva Nacional del Titicaca (Vallenas Gaona 2006).

Both Peru and Bolivia have seen a resurgence of left-wing political activity, and specifically indigenous left wing political activity, since the early 2000s. In Bolivia, this resulted in the election and government of Evo Morales from 2006 to 2019 (Mayorga, 2020). Morales, the first fully indigenous president of South America's only majority indigenous country, regularly won over 80% of the vote in La Paz Province, which includes the entire Bolivian shoreline of Lake Titicaca, though his party, the Movement towards Socialism (MAS in its Spanish acronym) often struggled in local elections, losing to the more explicitly *indigenista* Jallalla party in gubernatorial races (Torrez, 2021). Amongst the changes of the Morales government was recognition of the Andean conception of the earth as a living and divine being, the Pachamama, with rights, in the Bolivian constitution (Humphreys, 2017). In 2019. Morales was removed from office. After months of protests, much by indigenous people from the Altiplano, elections were allowed in 2020, which were won by MAS party candidate Lucho Arce, who remains the President of Bolivia. The revival of indigenous politics has also occurred, in more muted form, in Peru. A mix of a more fractured political landscape with more political parties, and the frequent arrest of Presidents due to corruption, has stymied wholesale cultural change as has occurred in Bolivia. Most recently, Pedro Castillo was elected in 2021. While elected on a primarily populist, rather than indigenous, platform, he won 88% of the vote in Puno Province.

After his removal in 2022, riots broke out across Puno Province. These protests were repressed, at the cost of a minimum of at least 60 dead protesters nationwide, including 18 in one incident in Juliaca, Puno Province (Calla Quispe, 2022).

While both Andean countries have had a revival in indigenous politics, in neither case has this revival led directly to more effective conservation measures for the Titicaca Grebe. In Peru this can be explained by the fact that indigenous political revival has never translated to overall control of national, or even regional, institutions. The same cannot be said of Bolivia. Some have accused the MAS governments of hypocrisy regarding the environment, as they have simultaneously lauded Andean cosmovision while continuing the "extractivist" political economy of Bolivia (Hope, 2016; Hope 2021). This is a biology, and not a politics, thesis, so I will not delve into this debate, except to say that in my experience indigenous people, like almost all people, consider increases material prosperity in the form of schools, clinics, and roads to be the primary motivation of political action. I also think that these critiques misunderstand both the nature of MAS. MAS has been successful precisely because it is not a purely indigenous political party, but it is a mixed socialist indigenous party, combining the two major strains of the Latin American left which so often are at loggerheads (Hale, 1994). Such a coalition can only be maintained by increasing living standards for ordinary people, including indigenous people – a goal which, given Bolivia position in the global economy as primarily an exporter of raw goods, could not be achieved without sacrificing in policy some of the environmental rhetoric of the early Morales government.

The Lake Titicaca Cultural Setting

Lake Titicaca forms the physical lynchpin of the Central Andean region, which is itself embedded in the wider Andean region. Much of the ethnobiological literature on the Andean region focuses on the impact of Andean cosmology, sometimes termed Andean cosmovision, on Andean people's interactions with nature (Gade, 1999; Graddy, 2013; Bédard, 2014; Sarmiento et al., 2018). This Andean cosmovision is attributed to the pre-Conquest worship of the Sun, referred to as Inti, and the earth, referred to as Pachamama, by the Quechua and Aymara speaking peoples of the Andes (Sarmiento, 2000; Mamani-Bernabé, 2015). More recently, this cosmovision has received formal legal approval from authorities in Andean nations, such as in Bolivia and Ecuador where the rights of the Pachamama have been enshrined in the constitution (Humphreys, 2017). This revived interest in Andean cosmovision has led to a growth in ethnobiology in Andean countries, especially in Bolivia, where Vice-President David Choquehuanca has appeared as a speaker at the Bolivian Society of Ethnobiology's conferences (González-Rivadeneira, 2023). However, this picture of Andean cosmovision simplifies the varied perspectives of Andean indigenous people towards nature, as I show later in this thesis. It also ignores the long history of cultural influence of European culture, and especially Roman Catholic Christianity (Seligmann & Fine-Dare, 2018), and more recently Protestant and Evangelical Christianity (Salas, 2018), on the indigenous people of the Andes.

The primary ethnic groups of Lake Titicaca are the Quechua and the Aymara. Roughly 70% of the rural population in the Altiplano is Aymara, and most of the remaining are Quechua. Quechua settlements are restricted to the northern shore of Lake Titicaca, from the city of Puno to the town of Moho. The modern Quechua population appears to descend from Quechuan settlers who moved to Lake Titicaca during the period of the Incan conquest, before the Spanish conquest (Stanish, 2003). The Aymara were resident in Lake Titicaca

before the conquest of the region by the Inca in the 14th century, and many Aymara claim that the ruins of Tiwanaku are the remains of a pre-Incan Aymara civilisation, though this has been contested by some archaeologists and linguists (Stanish, 2003; Heggarty, 2008; Sammells, 2013). The rural Aymara and Quechua have similar lifeways, with the majority of the population dedicated to traditional Andean agriculture of potato, quinoa, and oca. Historically fishing was rare amongst the Aymara and the Quechua (Young, 1997; Moore, 2011; Miller et al., 2021), but since the introduction of pejerrey and trout in the mid 20th century, fishing has become a more important industry amongst the lakeside Quechua and Aymara (Everett, 1973; Laba, 1979; Orlove et al., 1992; Orlove, 2002; Bruno et al., 2021), who have in Peru, more recently, taken to pisciculture.

The Uru are the only indigenous people of the Lake Titicaca region who historically relied primarily on the aquatic resources of the lake rather than agriculture (La Barre, 1941; Wachtel, 1978; Wachtel, 1986). Traditionally, the Uro lived on floating islands made of dried totora reed, and fished using nets of made of totora fibre and small canoes of totora reed (Orlove, 2002). According to both their own legends and genetic evidence, they are the longest residing ethnic group in Lake Titicaca (Kent, 2013; Sandoval et al., 2013). However, they were historically discriminated against, both before the Spanish conquest (Hemming, 2004), in the colonial period (Wachtel, 1978), and in the years since independence (La Barre, 1941; de la Barra Saavedra et al., 2011; Lara Barrientos, 2012). The Uru were outside the formal regime of Spanish taxes during the colonial period, and during the period of the Inca Empire they paid tribute in useless goods, such as frogs, showing the disdain which both conquerors had for them (Wachtel, 1986; Julien, 1987; Stanish, 2003). Much of this discrimination stemmed from the Uro's peculiar lifestyle, of living on floating totora islands etc., rather than on the lakeshore in settled villages. Because of lifestyle, the Uros primarily fished and hunted for sustenance,

rather than relying on agriculture like the neighbouring Aymara, Quechua, or Lupaca people who used to reside in the Lake Titicaca region before their amalgamation into the wider Aymara people in the colonial period (La Barre, 1941; La Barre, 1948; Wachtel, 1986).

More recently the Uru have, for the most part, abandoned fishing and hunting in favour of tourism. The Isla de los Uros in inner Puno Bay is now larger than any previously recorded Uru settlement, but it exists almost entirely for the purposes of tourism. When not hosting tourists on their floating islands, most Urus now live in the Chulluni neighbourhood of Puno, on the northern edge of the city. The move to tourism has caused conflict with the Reserva Nacional del Titicaca. Originally conflict between the Uru and the Reserva was around fishing and hunting rights in the protected area (Levieil & Orlove, 1990; Orlove, 1991; Orlove, 1993; Kent, 2008), but more recently it is about the encroachment of floating islands built for tourism into the Reserva.

Extensive anthropological and ethnobiological work has been done on the people of the Altiplano. In the early colonial period, chroniclers such as El Inka Garcilaso de la Vega described the tribute owed by the region around Lake Titicaca, which provides an indication to the pre-Columbian use of natural resources (Garcilaso de la Vega, 1617). Early naturalists in the Lake Titicaca region, such as Alcide d'Orbigny and Alexander Forbes, also wrote about the use of natural resources by local people (d'Orbigny, 1855; Forbes, 1870). The first ethnobiological surveys by a trained anthropologist were done by Weston La Barre, Bernard Mishkin, and Harry Tschopik Jr. in the 1930s and 1940s (La Barre, 1941; La Barre, 1946; La Barre, 1948; La Barre, 1951; Mishkin, 1946; Tschopik, 1946). Both Mishkin and Tschopik also died relatively young, in their 40s, limiting their contribution to the anthropology of the region. La Barre was a social anthropologist, but he wrote extensively about the traditional

fisheries and the use of medicinal plants by the Uru and the Aymara of the Lake Titicaca region (La Barre, 1946; La Barre, 1951). From the 1980s to today, most of the work on the ethnobiology of Lake Titicaca has been conducted by the partnership of Dominique Levieil and Benjamin Orlove. Between them they have written extensively on the fisheries of Lake Titicaca (Orlove et al., 1992; Orlove, 2002), changes in traditional ecological knowledge in the region (Levieil & Orlove, 1992; Orlove, 2002), and conflict between the local people of Lake Titicaca and government authorities (Levieil & Orlove, 1990; Orlove, 1991; Orlove, 1993). The Lake Titicaca region has a rich history of ethnobiological archeology, most of which stems from the long-standing Berkeley Taraco Peninsula archaeological site, researched by Christine Hastorf for over thirty years (Hastorf et al., 1992; Hastorf et al., 1998; Hastorf, 1999; Hastorf, 2015). Many students of Hastorf have continued to contribute to the archaeological ethnobiology of the Lake Titicaca basin, including Jose Capriles of Pennsylvania State University, Maria Miller of the University of Otago, and Maria Bruno of Dickinson College (Bruno et al., 2021; Capriles et al., 2008; Capriles et al., 2014; Miller et al., 2010; Miller et al., 2021). More recently, ethnobiological investigations have been undertaken by Peruvian and Bolivian anthropologists, such as Enrique Richard and Helga Gruberg (Richard & Contreras Zapata, 2018; Gruberg, 2022).

The Titicaca Grebe

Taxonomy

The Titicaca Grebe (*Rollandia microptera*) is an endemic Grebe found solely in Lake Titicaca and some of its connecting rivers and Lakes, such as Lake Umayo, River Desaguadero, River Ramis, and River Laka Jahuira (Konter, 2006; Martinez, et al., 2006;

Fjeldså, 2004; Fjeldså & Krabbe, 1990; Fjeldså, 1985; Fjeldså, 1981). It is an EDGE species, i.e., it is both endangered and part of an evolutionarily isolated lineage (Jetz et al., 2014). In this case, it is one of only two species in the genus *Rollandia*, together with the White-Tufted Grebe (*Rollandia rolland*), whose range extends from Tierra del Fuego to central Peru (Fjeldså, 2004). All grebes are members of the Podicipediformes, itself a monotypic order containing the single family Podicipedidae. The genus *Rollandia* is the most primitive extant genus of grebe (Ibid.). In past taxonomic revisions, *Rollandia microptera* has been variously described as a member of the genus *Podiceps* and of the monotypic genus *Centropelma* (Fjeldså, 2004; Sclater & Salvin, 1869; Gould, 1868)

Previous work on the Titicaca Grebe

Despite having been first described in 1868 (Gould, 1868), and erroneously redescribed a year later (Sclater & Scalvin, 1869), there is a dearth of scientific literature published on the ecology, behaviour, or other biologically salient details of the Titicaca Grebe. Nineteenth and early to mid-20th century naturalists and biologists who travelled to Lake Titicaca focused on listing the grebe as common, but did not write about its behaviour or ecology (Niethammer, 1953; Gilson, 1939; von Berlepsch & Stolzmann, 1906; Agassiz & Garman, 1875; Taczanowski, 1874; von Tschudi, 1870). The first papers on the ecology of the Titicaca Grebe had to wait over a century after its discovery, when what to this day remains the most comprehensive work on the biology of this species was written by Jon Fjeldså, comparing it to other Andean grebes (Fjeldså, 1985a; Fjeldså, 1985b; Fjeldså, 1981). Following Fjeldså, a few papers have been written on the population of the Titicaca Grebe (Martinez et al., 2006; Konter, 2006; Engblom et al., 2001), one on its seasonal movements in comparison to other waterfowl on the Peruvian side of Lake

Titicaca (Pulido Capurro, 2018), some work on whether the Titicaca Grebe could be a food source (Loza del Carpio et al. 2019), and some archaeological studies on grebe zooarchaeology (Steadman & Hastorf, 2015; Kent et al., 1999). Several non-peer reviewed studies on the Titicaca Grebe have also been written, including unpublished reports on its population from the Reserva Nacional del Titicaca (Gutiérrez Tito, 2009; Gutiérrez Tito & Arivilca Vilca, 2009), and a book chapter which primarily focused on how much less important it is culturally in the altiplano compared to other birds of the region, such as flamingos and condors (Richard & Contreras Zapata, 2018).

Behaviour, Ecology, and Morphology of the Titicaca Grebe

The Titicaca Grebe is usually 45-49 cm long, making it one of the largest grebes in South America (Fjeldså, 2004). It has a slender beak, typically 2.7-3.8 cm in length (Ibid.). Its usual weight range is unknown. Like almost all species of grebe, it exhibits almost no sexual dimorphism in terms of either size or colouration (Ibid.). The Titicaca Grebe is flightless, and according to at least one study, may have legs that are too weak to support it on dry land (Loza del Caprio et al., 2019), though this could also be due to the harsh conditions to which the grebes in that study were subjected. That said, I have never in my fieldwork seen a Titicaca Grebe walk on land, and I have heard of grebes stranded on land when the tide recedes, and being unable to escape dogs and rats.

Like almost all species of grebe, the Titicaca Grebe is piscivorous (Fjeldså, 2004; Fjeldså, 1981). It is a diving bird, though the depths and average duration of its dives remain unknown, as it was not considered ethical to tag birds in such a way

that individual identification at a distance would have been possible. The bulk of its diet, by weight, is native fish, especially *Orestias sp.*, found in Lake Titicaca, but it supplements its diet with insects and other invertebrates (Fjeldså, 1981). The Titicaca Grebe is most active feeding twice a day, first between 05:00 and 07:00, and then between 15:00 and 16:00 (Ibid.). It is a solitary hunter, and neither previous researchers nor I have found evidence of group hunting or other social behaviour beyond the familial unit.

Previous work suggested that the Titicaca Grebe is an opportunistic breeder, lacking a proper breeding season (Martinez et al., 2006). However, this has been disputed by some authors. While they agreed that the Titicaca Grebe can breed throughout the year, it most commonly does so in November and December, immediately after the end of the rainy season (Fjeldså, 1981). Though not a data chapter in this thesis, I can confirm the latter position, as nests with eggs are only observable in large numbers during and after the rainy season. Given that the timing of the rainy season and its end is changing due to climate change, I can confirm that the rains appear trigger breeding in this species, as finding nests with eggs appears to be independent of when in the calendar year the rainy season is. As in other grebes, the Titicaca Grebe builds a floating nest. It is highly territorial during breeding season, and fights are common between males of neighbouring territories (Konter, 2006; Fjeldså, 1981). Before my fieldwork, basic information such as the clutch size of the Titicaca Grebe was unknown. My own fieldwork confirmed it being 1 to 3 eggs, but also that a female can lay more eggs over the course of the breeding season to replace depredated eggs. It remains unclear how many broods the Titicaca Grebe can have over its lifetime. Both previous authors (Konter, 2006; Fjeldså, 1981) and I have observed alloparenting of chicks by juveniles, which suggests the possibility of stability in nest ownership and of familial units in this species over several years, but genetic

tests and longer term observations are needed to confirm if this is the case. The Titicaca Grebe has a large non-breeding population of non-territorial individuals (Fjeldså, 1981), primarily composed of 1st and 2nd year adults.

Conservation Threats to the Titicaca Grebe

When Fjeldså wrote his monograph on Andean grebes, the Titicaca Grebe was not considered endangered (Fjeldså, 1981). Indeed, while it had a highly restricted range, Fjeldså considered it one of the most common waterfowl on Lake Titicaca, and thought that its presence had a negative influence on other waterfowl, such as the White-Tufted Grebe and the Puna Teal (*Spatula puna*) with which he thought it competed (Ibid.). Twenty years later however, he considered the species to be endangered, and experiencing rapid declines in its population (Fjeldså, 2004). Since then, three surveys of the Titicaca Grebe's population have taken place. One, by Martinez et al. (2006) looked at a variety of sites in Lake Titicaca, and estimated a population of roughly 2,500 individuals across Lake Titicaca. Another, by Engblom et al (2001), noted a 70% decline in the grebe's population on the Peruvian side of Lake Titicaca between 1990 and 2000, and estimated that the population there stood at between 1,000 and 1,600. Finally, Konter (2006) found a Titicaca Grebe population of 1,100 individuals in the Laka Jahuira River, a tributary of the Desaguadero River on the Bolivian side, which is not thought to be a major habitat for the bird. No firm cause was established for the drivers of the decline, but habitat loss, fisheries bycatch, and invasive species were all listed as potential drivers of population declines.

Habitat loss is the main driver of biodiversity loss worldwide (Maxwell et al., 2016; Caro et al., 2022), and had been suggested as a potential driver of the decline in Titicaca Grebe numbers in the early 21st century (Engblom et al., 2001). Specifically, there was concern about the extent of totora wetland, which the Titicaca Grebe uses as its breeding habitat. These totora wetlands were semi-managed landscapes, due to the commercial value of totora in traditional Andean society (Banack et al., 2004). However, even twenty years ago scientists were beginning to notice a shift away from totora planting and management, and towards the use of commercially made goods (Ibid.). The suggestion was that the lack of human modification might have reduced the amount of semi-open totora mosaic upon which the Titicaca Grebe relies, and thus caused a reduction in its population. However my work (Chapter 2) found that while localised declines in totora have occurred in parts of Lake Titicaca, overall the amount of totora wetland has increased. We also addressed whether this decline on totora use had continued in Lake Titicaca (Chapter 4).

Of the three species of grebe which have gone extinct in the last fifty years, the extinction of two, the Atitlan Grebe and the Colombian Grebe, was linked to the introduction of invasive fish, especially salmonids (Wilmé, 1994; Fjeldså, 1993; Hunter, 1988). Invasive salmonids can cause population declines and extinctions in two main ways. The first is direct competition for smaller fish with the piscivorous grebes; this is the main way that introduced salmonids caused the extinction of the Atitlan Grebe (Hunter, 1988). Introduced salmonids can also have indirect effects on the ecosystem, which reduce grebe populations. Most South American grebes, unlike the Titicaca Grebe, rely heavily on macrozooplankton for their diet.

Salmonids, in addition to eating small fish, also eat macrozooplankton, and can change the limnofauna to become mainly microzooplankton. In this way, the introduction of salmonids caused the extinction of the Colombian Grebe (Fjeldså, 1993).

Most studies on the conservation status of the Titicaca Grebe agree that the greatest threat to the species is being caught as bycatch in fishermen's (especially monofilament) nets (Martinez et al., 2006; Konter, 2006; Engblom et al., 2001). Grebes are generally caught as they dive under water, and drown in the nets that prevent their resurfacing. However some are caught above the surface and instead starve to death. Previous studies on fisheries bycatch have found that even if technical solutions to bycatch can be found, implementation is impossible without the commitment of local people (Campbell & Cornwell, 2008; Psuty & Całkiewicz, 2021). We therefore focused our work on what drives attitudes towards the Titicaca Grebe (Chapter 3) and to address possible concerns of fishermen about the Titicaca Grebe (Chapter 6). We also focused on mapping fisheries across Lake Titicaca, and attempted to estimate fisheries bycatch using a combination of distribution modelling and social science approaches (Chapter 5).

Thesis Structure

This thesis is structured into eight data chapters, an introduction, and a conclusion. The introduction, which you have just read, introduces the importance of ethnobiology to understand social-ecological systems in the context of ecology, and goes on to introduce both the Lake Titicaca ecosystem and the rest of the thesis. Each of the data chapters addresses

either a different potential cause, or consequence, of the decline in Titicaca Grebe populations observed between the 1970s and the early 2000s (Engblom et al., 2001).

Chapter 2, "Trends in the area of suitable habitat for the Titicaca Grebe, 2001 – 2020", addresses whether population declines of the Titicaca Grebe could be due to declines in available habitat. Given that habitat loss is the main driver of biodiversity loss worldwide (Maxwell et al., 2016; Caro et al., 2022), and the uncertainty regarding the potential of travel due to COVID-19 at the start of this thesis, it seemed prudent to begin with this hypothesis. It used satellite data to map the extent of potential breeding territory of the Titicaca Grebe, and found that there had been no significant change in habitat extent, ruling out habitat loss as a major driver of population declines.

Chapter 3, "Estimating the Global Population Size and Highlighting Conservation Priority Areas for the Endangered Titicaca Grebe", is the result of field surveys for the Titicaca Grebe done from March to September 2022. It is the first update on the population of the Titicaca Grebe across its range since 2003, and shows that the population has likely increased since the last range wide population assessment. However, it also shows that the population is below the peak recorded in the 1970s, suggesting that there either there are still significant pressures on the population of this species, or that it has not fully recovered from past anthropogenic pressures.

Chapter 4, "Indigenous-Wildlife Conflict and Coexistence in the Altiplano", focuses on the social aspects of the Lake Titicaca ecosystem. It consists of a series of surveys done with local people in the Lake Titicaca region to address attitudes towards the Titicaca Grebe which might help, or hinder, conservation efforts. I found that the vast majority of the population was

apathetic towards the grebe, but that a significant minority was actively hostile. This hostile minority was disproportionately fishermen, who disliked the grebe for breaking their nets and for competing with them for fish.

Chapter 5, "Declining Use of Totora (*Schoenoplectus californicus* subsp *tatora*) in Lake Titicaca" returns the focus to the breeding habitat of the Titicaca Grebe. Totora wetlands are, like much of the Andes, a cultural ecosystem (Ellenberg, 1979; Erickson, 2000). They are important for biodiversity, but they are an ecosystem whose origin and maintenance is tied with indigenous management practices. This chapter focuses on changes in these management practices, and the causes of the abandonment of traditional management practices by indigenous people.

Chapter 6, "Combining Modelling and Social Science Approaches to Understand Artisanal Fisheries Bycatch in Lake Titicaca", is an attempt to quantify the extent of fisheries bycatch of the Titicaca Grebe. Having found that bycatch is one of, if not the, major threat towards the Titicaca Grebe, I found it necessary to try to quantify its commonality. However, it didn't prove practicable to have an entire monitoring system of the fisheries of Lake Titicaca. Instead, I attempted to combine net surveys, interviews, and distribution modelling to estimate the frequency of fisheries bycatch in Lake Titicaca. I found that fishers seem to exaggerate fisheries bycatch in this system, leading to biologically implausible estimates, but that distribution modelling can accurately model artisanal fisheries.

Chapter 7, "Addressing conflict between fishermen and the Titicaca Grebe (*Rollandia microptera*) through diet analysis", is an attempt to address one of the material bases of fisher-grebe conflict, namely the fear that the Titicaca Grebe is in competition for choice fish with

fishermen. Using a combination of stomach content and interview data, I found that there was some overlap in the target fish of fishers and grebes, but that the bulk of this overlap was in the less commercially important native *Orestias* sp. species.

Chapter 8, the Discussion, draws together the data chapters into a coherent whole. It also discusses some of the limitations of this present work, and what future research avenues exist for the study both of the Lake Titicaca ecosystem. It also discusses the important of this work in the wider context of integrating ethnobiology and local voices into ecology and conservation, and what implications this work could have for researchers in other systems.

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2

Trends in the area of suitable breeding habitat for the Endangered Titicaca Grebe *Rollandia microptera*, 2001–2020

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Trends in the area of suitable breeding habitat for the Endangered Lake Titicaca Grebe *Rollandia microptera*, 2001–2020

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Summary

The Lake Titicaca Grebe *Rollandia microptera* is a poorly studied endemic species found in the Lake Titicaca watershed of Peru and Bolivia. Multiple surveys from the early 2000s indicated that the species was suffering a rapid population decline with an unknown cause. At the same time as these surveys, reports emerged that there was an increase in burning of the totora wetlands which are thought to be the primary habitat for the Lake Titicaca Grebe. However, since 2003, no work has been published either on the current population of the Lake Titicaca Grebe, or the extent of the totora wetlands in the Lake Titicaca region. This paper used satellite data to monitor the change in extent of habitat potentially suitable for the Lake Titicaca Grebe to determine whether habitat loss is likely to be a major driver of population declines in this species. We found that the extent of potentially suitable wetland remained stable between 2001 and 2020, though there are more local regional trends of change in extent of totora. We also found that multiple areas exist that might support Lake Titicaca Grebe populations, but where ornithological knowledge is lacking. We suggest no change to the IUCN status of the Lake Titicaca Grebe, but recommend that further fieldwork is required to monitor the species' current population, especially in previously unstudied but potentially habitable areas.

Introduction

Conservation planners and practitioners need good information about species population sizes and ranges when deciding how to allocate limited resources, in order to maximise the efficacy of their conservation efforts (Bottrill *et al.* 2008). However, such data are not often available, especially for those species that live in fragmented ranges, or which are not subject to consistent and long-term monitoring (Canessa *et al.* 2015, Franklin 2010). Whilst recognising the need for "ground-truthing", satellite remote-sensing data have become increasingly important to fill gaps in conservation knowledge, since they offer a way to collect ecological information over a wide temporal and spatial scale without requiring people on the ground to monitor a species or habitat (Rose *et al.* 2015). Satellite remote sensing has been used in conservation science to estimate the change in the range and population of various species, including waterfowl (Harrity *et al.* 2020, Long *et al.* 2008), to track the rate of degradation of specific ecosystems (Alonso *et al.* 2016), and to measure the efficacy of ecosystem restoration projects (Cordell *et al.* 2017). We used satellite remote sensing to determine the extent of change in the potential habitat of the Endangered Lake Titicaca Grebe (*Rollandia microptera*) since 2001.

The Lake Titicaca Grebe is endemic to the binational watershed of Lake Titicaca, in Peru and Bolivia (Fjeldså 2004, Fjeldså and Krabbe 1990, Fjeldså 1981), whose conservation status is ranked as "Endangered" (BirdLife International 2021b). It is a member of the monophyletic family Podicipedidae of the order Podicipediformes, a group of conservation priority (O'Donnell and Fjeldså 1997), due in large part to the inability of many species to adapt to anthropogenic disturbances through their reliance on wetlands and low propensity to disperse (O'Donnell and Fjeldså 1997, Fjeldså 1984). This vulnerability to anthropogenic change is especially pronounced for endemic grebes isolated in one or a few lakes, of which three, the Atitlan Grebe (*Podilymbus gigas*), the Colombian Grebe (*Podiceps andinus*), and the Alaotra Grebe (*Tachybaptus rufolavatus*), have gone extinct in the last 50 years (BirdLife International 2021a, Fjeldså 1993, Hunter 1988). In addition to its endemicity, the Lake Titicaca Grebe has been singled out as a conservation priority because it is an Evolutionarily Distinct and Globally Endangered (EDGE) species (Jetz *et al.* 2014).

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Few surveys have been carried out to provide an adequate baseline figure for its population. However, a series of censuses from the early 2000s suggested that the species was experiencing a rapid population decline (Martinez *et al.* 2006, Konter 2006, Engblom *et al.* 2001 unpublished). Martinez *et al.* (2006) suggested that the main driver of this decline was by-catch from monofilament nets that had become increasingly popular around Lake Titicaca. However, although by-catch is undoubtedly a major threat to the species, it is just one of many potential forces that could be reducing the grebe population, including increased pollution in Lake Titicaca (Ibarguchi 2014, Rieckermann *et al.* 2006), competition with introduced salmonids as has harmed other endemic grebe species (Martinez *et al.* 2006), and potentially also habitat loss. This last driver is considered important because of a recent rapid lowering of the water level in some of the outlying parts of the Lake Titicaca watershed, especially in Lake Poopó and parts of the Desaguadero River (Perreault 2020, Torres-Batlló *et al.* 2020).

The Lake Titicaca Grebe is entirely aquatic, since its legs appear to buckle when on dry land (Loza-del Carpio *et al.* 2019), and its wings are too weak to allow it to fly. It is piscivorous, and forages mainly in open water far from the lake shore (Fjeldså 1981). However, it spends its evenings and its breeding period closer to the shore, relying on the wetlands, and especially wetland mosaics, for nesting (Fjeldså 1981). The species is highly territorial, and large numbers of aggressive unpaired individuals that lack territories may be challenging territory holders (Fjeldså 1981). This suggests that the extent of potential breeding habitat around Lake Titicaca is a limiting factor for the grebe's population. The species appears to be well adapted to take advantage of any new breeding territory which may occur due to changes in water level, as shown by the existence of a large breeding population in the seasonally dry Laka Jahuira River during the rainy season (Konter 2006), and observations of grebes colonising parts of the Lake Titicaca floodplain that are temporarily flooded during the rainy season (Fjeldså 1981).

Authors disagree as to how best to categorise the different zones of aquatic vegetation in Lake Titicaca. Iltis and Mourguiart (1992), Raynal-Roques (1992), and Guerlesquin (1992) separated Lake Titicaca into three broad aquatic vegetative zones; totora wetland, llacho, and chara, while Tutin (1940) separated it into the *Zanichella–Potamegaton* Association, the *Myriophyllum–Elodea* Association, the *Chara* Association, and the *Sciaromium* Association. Totora areas are dominated by sedges, chiefly *Schoenoplectus californicus*, but with some *S. acutus*, which can grow several metres above the surface of the water (Raynal-Roques 1992). In the late twentieth century totora wetlands were amongst the most common around Lake Titicaca (Iltis and Mourguiart 1992), but earlier work suggested totora limited to sheltered bays and did not constitute an important ecosystem of its own, instead being superimposed locally on to the *Myriophyllum–Elodea* Association (Tutin 1940), suggesting a significant expansion in the twentieth century. Llacho areas are dominated by *Myriophyllum* spp. and *Elodea* spp. (Iltis and Mourguiart 1992). Llacho areas are characterised by milfoils and other softer aquatic plants which often occur more clumped in distribution than totora, and float near the surface (Iltis and Mourguiart 1992). Chara (*Chara* spp.) is an alga which occurs frequently in Lake Titicaca (Guerlesquin 1992). Historically chara was limited to depths of 9–12 m (Tutin 1940), but more recently blooms of chara have occurred on the surface of the lake, albeit still in areas where lake depth is too great for totora or llacho (Guerlesquin 1992). The *Myriophyllum–Elodea* Association includes what later authors referred to as totora and llacho. The *Chara* Association corresponds to the chara as described by Guerlesquin (1992). The *Zanichella–Potamegaton* Association and the *Sciaromium* Association are both sub-aquatic and irrelevant for this study.

Of the main types of wetland around Lake Titicaca, there is debate as to whether totora or llacho is the more important breeding habitat for the Lake Titicaca Grebe. Fjeldså (1981), Fjeldså (2004), Kent *et al.* (1999), and Pulido Capurro (2018) considered the totora wetland to be the main breeding habitat of the Lake Titicaca Grebe, considering it sympatric with the White-tufted Grebe (*Rollandia rolland*), which is also found in the totora. However, Martinez *et al.* (2006) considered the totora to be less important as a breeding habitat for the Lake Titicaca Grebe than the less dense llacho-dominated landscapes, a view supported by recent observations by author EGMT. Furthermore, there is some palaeoecological evidence that grebe bones correlate with totora seeds, suggesting that the extent of totora has influenced the grebe population in the past (Bruno *et al.* 2021). In this paper we focus on the extent of the totora wetlands since we cannot differentiate between chara or other algal vegetation and llacho using satellite imagery. Whilst this may risk underestimating the potential area of habitat suitable for the Lake Titicaca Grebe, it is generally agreed that chara is not an important habitat for the species, and we considered it prudent to focus on the most likely potential habitat.

Historically, the extent of totora around Lake Titicaca has been heavily managed by the indigenous communities that surround the lake (Banack *et al.* 2004, Stanish 2012, Erickson 2000, Levieil and Orlove 1990, 1992). Totora has been harvested by the local people for at least 3,500 years (Erickson 2000), and has been used for the construction of houses, boats, and as feed for cattle, sheep, and, historically, for llamas. The harvesting of totora is traditionally tightly regulated by the extended local families in each village, also called *ayllus* (Levieil and Orlove 1990, La Barre 1948), and disputes over totora used to be frequent in the area around Lake Titicaca (Levieil and Orlove 1990, La Barre 1948). Totora harvesting is usually restricted to the dry season when fresh green totora is rare (Banack *et al.* 2004, Heiser, 1978, La Barre 1948, Tutin 1940). This harvesting breaks up the dense totora wetlands and creates a mosaic with open water channels which may be a seasonally important habitat for the Lake Titicaca Grebe. However, the growth of construction from concrete and increased use of modern boats appears to have reduced the economic importance of totora (Orlove *et al.* 1992), and in turn weakened many of the traditional controls on its harvesting (Banack *et al.* 2004, Levieil and Orlove 1990). Even the water dwelling Uru Uru, the ethnic group who traditionally most relied on totora from the lake (La Barre 1941), appear to have abandoned the use of traditional totora boats, apart from showing them to tourists (Stanish 2012). Palaeoecological evidence suggests that wetlands around Lake Titicaca were much more extensive in the past, especially at the height of the Tiwanaku civilisation around the lake (Erickson 2000), suggesting that the extent of totora has been influenced by the economic activities of the area for several thousand years. There is evidence of burning of totora fields as the plant is no longer valued economically by villagers around the lake (Stanish 2012), but the extent of these burnings is unclear.

While humans are a significant influence on the extent of totora around Lake Titicaca, they are not the only factor that influences totora extent. Given the nature of the totora plant, lake depth is also important, both on a seasonal and a long-term basis (Moreau *et al.* 2003). Since the introduction of totora by humans between 3,500 and 5,000 years BP (Erickson 2000, Heiser 1974), Lake Titicaca has experienced fluctuations in lake levels which mean that the lake level has at times been over 70 m lower than the present level

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(Weide *et al.* 2017, Baker and Fritz 2015, Baker *et al.* 2001, Mourguiart *et al.* 1998). In the twentieth century alone there has been a 7-m change in the lake level (Hampton *et al.* 2018), and there have been periods of significant flooding which has influenced the extent of aquatic vegetation in the region (Hampton *et al.* 2018, Pawley *et al.* 2001). Furthermore, the wider altiplano was covered extensively by lakes and wetlands for much of the Pleistocene (Placzek *et al.* 2011, Rigsby *et al.* 2005, Cross *et al.* 2001), and the fact that the Lake Titicaca Grebe is a phylogenetically basal species suggests that it existed through this much wetter period in the altiplano (Fjeldså 1981). In addition to these long-term changes in lake level, Lake Titicaca experiences seasonal variations in lake level associated with precipitation causing the lake level to vary by up to several metres within the course of a single year (Lima-Quispe *et al.* 2021, Moreau *et al.* 2003). This long-term history of volatility in water levels and associated vegetation communities means it is likely that the Lake Titicaca Grebe has evolved behavioural mechanisms to rapidly colonise temporary breeding grounds. These temporary patches of totora in turn can act as bridges between otherwise isolated populations of Lake Titicaca Grebe, for instance those that exist in Lake Arapa and Lake Umayo.

Methods

Study area

Lake Titicaca is a large freshwater lake bridging Peru and Bolivia. The lake has a surface elevation of 3,812 m, and a surface area of approximately 8,372 km^2, although this has varied greatly over time. The lake forms the core of the Lake Titicaca basin, a large and relatively flat part of the Andes, known as the altiplano. Several rivers feed into Lake Titicaca, including the Desaguadero River and the Ramis River, as well as several large lakes that connect or until recently connected with Lake Titicaca, including Lake Poopó, Lake Uru Uru, Lake Arapa, and Lake Umayo.

Dataset

Granules of Landsat 4, 5, 7, and 8 data from the United States Geological Survey (USGS), were acquired from 2001 to 2020, inclusive. We used WRS-2 path 233 and rows 71–72, and WRS-2 path 1 and rows 71–72. These tiles cover both Lake Titicaca itself, and the various rivers and outlying lakes that make up its watershed, including the Desaguadero River and the Laka Jahuira River, both of which supported Lake Titicaca Grebe populations in the past (Engblom *et al.* 2001 unpublished, Konter 2006). Each pixel has a resolution of 30 m × 30 m, which allows us to detect all but the smallest stands of totora.

Pixel level quality assurance information was used to mask clouds and hence used temporal compositing to calculate mosaics of the annual mean surface reflectance from all valid observations in six wavebands: blue, green, re, nir, mir1, and mir2. We excluded the year 2011 as there were too few valid cloud-free observations acquired in this year.

Classification and validation

All data analysis was carried out in TerrSet, version 19. We used ground reference data provided by author ERGT on the distribution of totora and open water in the Bahia de Puno in 2020 and 2013. The 2020 data were used to train the classifier; the 2013 data were used to validate the model.

Linear spectral unmixing (Settle and Drake 1993) was used to estimate the proportion of each pixel comprising the end-members totora and water, and then hardened the result to a categorical map. This classification was restricted using a mask to the area of the wetland ecosystem. We then measured the accuracy of the model using Cohen's kappa, which measures the accuracy of the classifier on a random set of marked pixels not used in the creation training or testing of the classifier while taking into account the odds of correct results occurring due to chance (Congalton and Green 1999). Finally, we counted the number of pixels classified as totora in each year to derive our area estimates.

Following the logic of Long *et al.* (2008) and Mladenoff and Sickley (1998), population estimates for each year were obtained by multiplying the area of totora by the average population density found across their study sites by Martinez *et al.* (2006) with the area we found. Finally, we used the standard deviations of the grebe's population density reported by Martinez *et al.* (2006) to estimate uncertainty. This population estimate assumed that the Lake Titicaca Grebe uses the entirety of the totora wetlands of Lake Titicaca as their breeding territory. We consider that the evolutionary history of the Lake Titicaca Grebe, as well as observations of the species in temporary areas of suitable breeding territory (Konter 2006, Fjeldså 1981), suggest that the species is able quickly to colonise areas of totora.

Although previous population surveys failed to discover any significant areas of totora where the Lake Titicaca Grebe was absent, it is clear that other species, such as *R. rolland*, compete with the Lake Titicaca Grebe for breeding sites in the totora (Fjeldså 1981); *R. rolland* prefers to nest in landward areas and *R. microptera* in lakeward areas. We therefore also provide a more conservative estimate of the potential population of the Lake Titicaca Grebe, which assumes that the species occupied only half of the potential breeding territory of the totora. While we recognise that this percentage of totora occupation is arbitrary, the lack of literature describing the percentage of territory in totora occupied by different species of waterfowl as breeding territories effectively renders any percentage of the totora being occupied by the grebe as arbitrary and so we consider a conservative estimate justified.

Plots for the extent of totora and potential population of the grebe were constructed using the programme "R". For both the population and the area of totora, a change was considered significant if it was greater than the 95% confidence interval of the figures for each year.

Results

The Cohen's kappa of our classifier for totora of 0.91 indicates excellent accuracy. Contrary to expectation, we found no discernible decline in the extent of totora around Lake Titicaca since 2001. Instead, we observed that the extent of totora appeared stable, with most years not observing any change that was greater than the uncertainty of the area estimate (Figure 1). Although in a few years (e.g. 2004 and 2014) the extent of totora in the watershed had declined, this decline was less than the uncertainty in the area estimate, and overall the extent of totora increased by more than the area uncertainty estimate between 2001 and 2020.

Observed population densities of the Lake Titicaca Grebe (Figure 2) have been extremely variable, ranging from 35.4 individuals/km^2 to 0.5 individuals/km^2; even excluding these extreme values, the species appears to have a very variable population density, averaging around 6.1 individuals/km^2. As such, our

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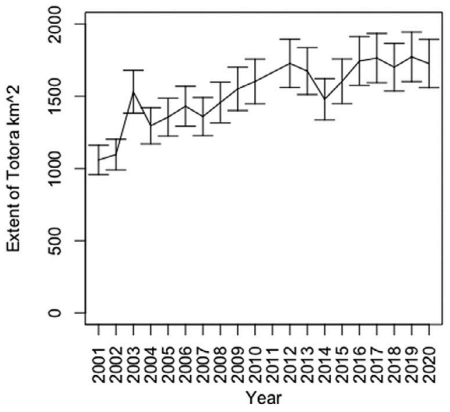


Figure 1. Change in the extent of totora in the Lake Titicaca watershed, 2001–2020, according to the model developed in this paper. The error bars depict the 95% confidence interval of the extent of totora in the Lake Titicaca watershed.

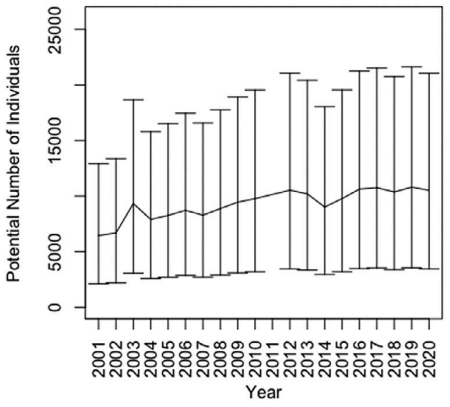


Figure 2. Potential population of the Lake Titicaca Grebe, 2001–2020, determined by multiplying the potential habitat area by the average population density of grebes found by Martinez *et al.* (2006), assuming grebes occupy the entirety of the totora. Error bars come from the standard deviation in the size of Lake Titicaca Grebe found by Martinez *et al.* (2006).

estimates for the potential population of the Lake Titicaca Grebe vary widely, ranging from a potential minimum of 2,118 individuals in 2001 to a potential maximum of 21,626 in 2019, assuming that the species occupies the entirety of the totora wetlands. Our more conservative population estimate, which assumes that the grebe occupies half of the potential breeding habitat (Figure 3), showed the same pattern of change in potential population, with a potential minimum of 1,054 individuals in 2001 and a potential maximum of 10,813 individuals in 2019. In neither of our more liberal conservation population estimates did the population size of the Lake Titicaca Grebe exceed the 95% uncertainty of its population, meaning that there was no statistically significant change in potential population of the Lake Titicaca Grebe between 2001 and 2020 according to our study.

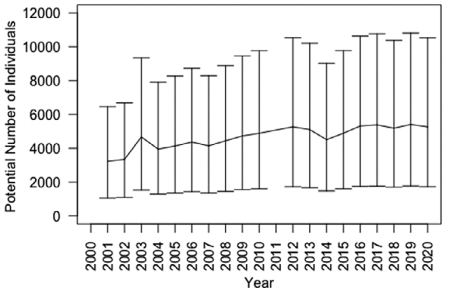


Figure 3. Potential population of the Lake Titicaca Grebe, 2001–2020, determined by multiplying the potential habitat area by the average population density of grebes found by Martinez *et al.* (2006), assuming grebes occupy half of the area of totora. Error bars come from the standard deviation in the size of the Lake Titicaca Grebe found by Martinez *et al.* (2006).

The location of the totora wetlands appears to have changed slightly during our period of study. In spite of a documented rise of pollution in the area (Beltrán Farfán *et al.* 2015), an increase in totora in the Puno Bay area is apparent. Totora may be resilient to heavy metal pollution (Blanco 2019), and the Puno Bay area is part of the Reserva Nacional de Titicaca. This is an officially protected area in Peru, even if an underfunded one, since it suffers regularly from incursions from illegal fisheries and totora harvesting. An apparent increase in totora extent at the mouth of the Desaguadero River is also discernible. This is another well-established area for the Lake Titicaca Grebe. We detected evidence for a reduction in the extent of totora in the Laka Jahuira River which is consistent with the drying up of Lake Poopó over the course of this study. One of the most stable totora habitats appears to be in the Ilave River and its tributaries, which to our knowledge have not been surveyed for Lake Titicaca Grebe. Finally, we also identified several areas in Lake Titicaca where totora appears to be extensive and stable (Figure 4). These areas are probably home to breeding populations of the Lake Titicaca Grebe, and should be the focus of future population surveys of this species (Figure 5).

Discussion

Population estimates of the Lake Titicaca Grebe are necessarily based on limited data. However, we have established through satellite imagery that the Lake Titicaca watershed includes enough totora wetland for a potential population of up to tens of thousands of individuals. Other factors, such as pollution and fishing pressure, might be expected to reduce numbers substantially below this potential carrying capacity. Nevertheless, it is significantly greater than the estimates of 250–999 individuals on which BirdLife International's (2021b) conservation status of Endangered was based. Even the more conservative potential population figure suggests a population of up to about 5,000 individuals. This is not the first suggestion that the Lake Titicaca Grebe population might exceed that on which the IUCN categorisation was made. Both surveys of the Lake Titicaca Grebe made two decades ago identified more than 1,000 individuals. A survey in 2003 estimated at least 2,582 individuals at 22 sites across Lake Titicaca (Martinez *et al.* 2006), while a later survey identified 1,100 individuals living in the Laka Jahuira

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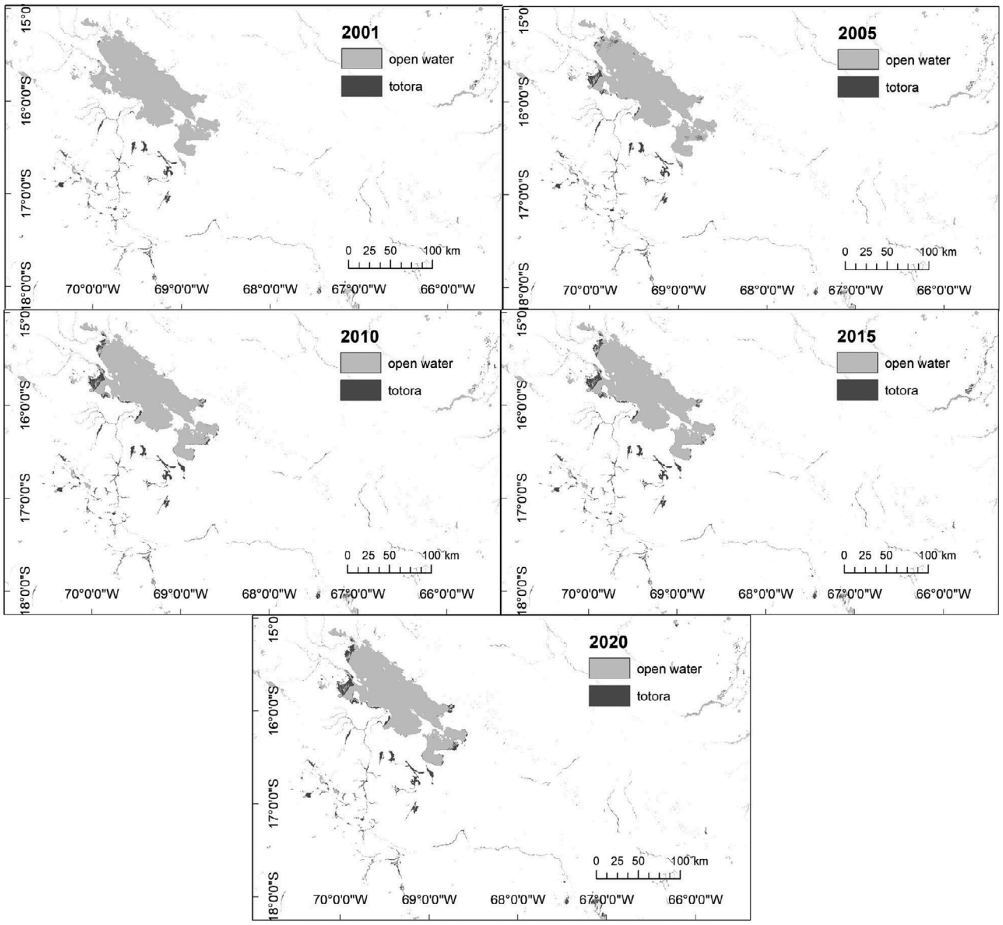


Figure 4. Selected maps showing the change in the extent of totora in the Lake Titicaca watershed. Maps show the results of our model which shaded each granule as being either totora or open water.

River, a tributary of Lake Titicaca which is not thought to be a major population centre for the species (Konter 2006).

Despite the age of these surveys, it would require a precipitous population decline of over 50% to reduce a population of several thousand in one portion of the lake to fewer than 1,000 birds in the species' entire range in 15 years. Whilst not unprecedented in other species (Menz and Arlettaz 2012, Wiles *et al.* 2003, Hutchings 2000), including grebes (Dinesen *et al.* 2019, Guevara *et al.* 2016, Fjeldså 2004), we suggest that firmer evidence is necessary before such a precipitous decline could be declared, especially when the species continues to be sighted regularly around Lake Titicaca (DAV, pers. obs.). Whilst possible, the apparent availability of suitable habitat suggested by our study indicates that further surveys are urgently required to inform the IUCN categorisation of the Lake Titicaca Grebe.

Further corroborating evidence that the IUCN estimate of the Lake Titicaca Grebe's population size may be underestimated comes from reported incidences of by-catch by fishermen and from modelling of global bird abundances. Whilst no comprehensive data exist on the number of birds caught as by-catch by fishermen in Lake Titicaca, it is known that grebes are caught frequently in monofilament nets. Martinez *et al.* (2006) suggested that most Bolivian fishermen catch a grebe as by-catch every fortnight. As with the population of grebes, there are no recent published statistics on the number of fishermen around the lake. In 1992, it was estimated that some 3,000 individuals derived their main income from fishing in the Lake Titicaca area (Orlove *et al.* 1992). They did so in crews that consisted mainly of either solitary or pairs of fishermen (Orlove 2002), but the number has probably increased in parallel with the increase in the general population around the

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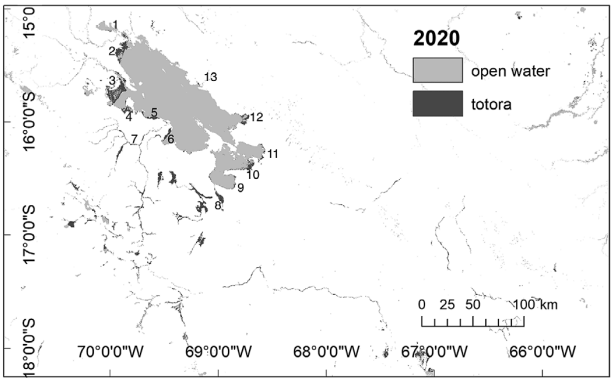


Figure 5. Detailed map of sites of extensive totora coverage in or connected to Lake Titicaca in 2020. 1: Lake Arapa, Peru; 2: Reserva Nacional del Titicaca, Peru; 3: Puno Bay, Peru; 4: Chucuito, Peru; 5: Ariputi, Peru; 6: Juli, Peru; 7: Ilave River, Peru; 8: Desaguadero River, Peru and Bolivia; 9: Guaqui, Bolivia; 10: Batallas, Bolivia; 11: Puerto Perez, Bolivia; 12: Achacachi, Bolivia; 13: Escoma, Bolivia.

lake. It is unclear how these figures relate to rates of by-catch and the grebe's population dynamics. However, modelling of global bird abundances places the likely population of Lake Titicaca Grebes at around 8,887 individuals (Callaghan *et al.* 2021). This is almost halfway between our liberal population estimate based on the assumption that the grebe occupies the entirety of its potential breeding habitat, and our conservative estimate based on its occupation of half the potential breeding habitat. It suggests therefore that the species may occupy most, though not all, of the totora wetlands as breeding territory.

Although we suggest that the population may exceed the IUCN population estimate, we do not recommend a change in its IUCN threat category at this time for two reasons. First, our analysis can only suggest a potential grebe population size based on the little we know of its breeding habitat preferences. Further research into habitat preference may suggest a smaller potential population. Secondly, our analysis does not consider the intensity of fishing around the lake. Given that by-catch from monofilament nets is thought to be the greatest threat to the Lake Titicaca Grebe (Martinez *et al.* 2006), that fishing with monofilament nets is a relatively recent phenomenon which lacks a history of sustainable management like many other indigenous fisheries have, and that much of such fishing occurs in marshes that surround Lake Titicaca (Orlove 2002, Orlove *et al.* 1992), it is likely that much of the area whose vegetation is suitable for the Lake Titicaca Grebe fails to support grebe populations because of fishing.

We suggest that future research should involve greater direct population monitoring of the grebe. This should include extensive population surveys, since no survey of the whole lake area has been undertaken since 2003 (Martinez *et al.* 2006). Any change in the IUCN category of the species must be based on observed population change. Any population survey would have to include the Ilave River, since our study suggests this potentially offers much suitable habitat for the Lake Titicaca Grebe. Finally, extensive study should be undertaken to quantify the impact of fishing by-catch on the population. Only by such intensive re-evaluation might the IUCN categorisation be informed.

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Estimating the Global Population Size and Highlighting Conservation Priority Areas for the Endangered Titicaca Grebe

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RESEARCH ARTICLE

Global population size and conservation priority areas for the endangered Titicaca grebe

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Abstract

The Titicaca grebe (*Rollandia microptera*) is a poorly studied endangered species, only found in the Lake Titicaca watershed of Peru and Bolivia. Population surveys undertaken in the early twenty-first century suggested that the species had declined in number by >70%. We conducted a population survey of the grebe between March and August 2022 in Peru and Bolivia, using both maximum entropy and Bayesian occupancy models to estimate factors affecting habitat suitability for the grebe. We conducted surveys between March and August 2022 in Peru and Bolivia. Contrary to the International Union for Conservation of Nature (IUCN) population estimates of <1,000 individuals, there are likely tens of thousands of individual grebes. The population estimation was sensitive to the type of model used. Distance from shore and fishing intensity were the most significant factors influencing grebe populations. The Reserva Nacional del Titicaca, the only protected area in the lake, covers some of the most suitable Titicaca grebe habitat across its entire range. The population of the Titicaca grebe is significantly higher than previous estimates, but we do not recommend a change to its conservation status because of the lack of conservation efforts for this species, and the

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long-term risks associated with global warming and fisheries bycatch.

KEYWORDS
Bolivia, conservation, density estimation, habitat use, Lake Titicaca, Peru, population census, *Rollandia microptera*

Ecology and conservation biology require accurate information on the abundance and distribution of species (Shaffer 1981, Katzner et al. 2011). Although knowledge of population size is important to establish which species are of conservation priority (Rodrigues et al. 2006), it is especially so for species with restricted ranges or small populations because they are particularly sensitive to environmental change (O'Grady et al. 2004, Harris and Pimm 2008).

While the entire world is undergoing a crisis of biodiversity loss (Cowie et al. 2022, Lees et al. 2022), that loss is occurring at an uneven rate. The tropical Andes, including Lake Titicaca, is one of the most vulnerable ecosystems to climate change in the world (Trew and Maclean 2021). Freshwater ecosystems, which are highly threatened (Strayer and Dudgeon 2010, Reid et al. 2019), poorly studied (Dudgeon et al. 2006, Şekercioğlu et al. 2012, Maasri et al. 2022), and poorly protected (Albert et al. 2021), also suffer from funding and research neglect. This is especially true for freshwater wetlands, such as those that comprise much of the habitat of the Titicaca grebe (*Rollandia microptera*; Villar et al. 2023), the loss of which is 3 times greater than that of global deforestation (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2019).

Protected areas remain an important asset for species conservation (Rodrigues and Cazalis 2020), but they can have drawbacks; they may potentially cause conflict with local communities (Adams and Hutton 2007, Dowie 2009, Şekercioğlu 2012), have boundaries based on political or aesthetic considerations rather than ecological ones (Runte 2010), or no longer offer protection to the ecosystems they are designed to protect because of the effects of global warming (Hannah 2010). In countries where conservation funding is not a government priority, there is also the issue where protected areas exist legally but are either unenforced, or minimally enforced (Brown and Mitchell 2000, Rife et al. 2013). A portion of Lake Titicaca has been a protected area since the founding of the Reserva Nacional del Titicaca in Peru in 1978. The Reserva has had some conservation successes and is involved in teaching local communities about the value of the wildlife in Lake Titicaca. Since its inception, there has been social strife leading to conflict between the Peruvian park authorities and local people (Orlove 1991, 2002; Kent 2006, 2008). These conflicts, which have primarily revolved around hunting and fishing rights, and the right to collect totora (*Schoenoplectus californicus tatora*), a sedge of traditional economic and cultural value (Villar et al. 2024*a*), have led to violence (E. R. Gutiérrez Tito, Servicio Nacional de Áreas Naturales Protegidas por el Estado, personal observation). Nevertheless, for several decades, a *modus vivendi* has been established between the Reserva and local communities. Similar approaches to traditional resource extraction within national parks have been used in other contexts to justify areas as protected, or have been found to be counter-productive to conservation goals (Redford and Sanderson 2000, Exton et al. 2019, Acreman et al. 2020).

In addition to its importance as the habitat of the Titicaca grebe, the Lake Titicaca ecosystem is a globally important freshwater biodiversity hotspot. Ninety-two percent of all the fish species in Lake Titicaca are endemic (Albert et al. 2011), many of which are endangered or thought to be extinct because of the introduction of invasive species, such as rainbow trout (*Oncorhynchus mykiss*) and pejerrey (*Odontesthes bonariensis*; Lauzanne et al. 1992, Vila et al. 2007). Lake Titicaca is also a global hotspot for invertebrates, having been highlighted as 1 of the 20 most important freshwater ecosystems for global malacological biodiversity (Strong et al. 2008).

The area has extensive high-altitude wetlands containing totora sedge (Iltis and Mourguiart 1992), which provide the primary nesting habitat of the Titicaca grebe (Villar et al. 2023). Consequently, the region is considered an important bird area (BirdLife International 2024*a*), and the wetlands have been listed under the Ramsar

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Convention for decades (Sarmiento 1998). Nevertheless, they are considered at risk due to anthropogenic change (Riedinger-Whitmore et al. 2023).

The Titicaca grebe, considered endangered by the International Union for Conservation of Nature (IUCN), is endemic to Lake Titicaca and surrounding bodies of water, in Peru and Bolivia (Fjeldså and Krabbe 1990; Fjeldså 1981, 2004; Martinez et al. 2006; Villar et al. 2023). It is a member of the family Podicipedidae of the order Podicipediformes, a group of high conservation priority that is particularly vulnerable to anthropogenic disturbances (Fjeldså 1984, O'Donnell and Fjeldså 1997). In the last 50 years, 3 grebes (2 in South America) have gone extinct: the Atitlan grebe (*Podilymbus gigas*), the Colombian grebe (*Podiceps andinus*), and the Alaotra grebe (*Tachybaptus rufolavatus*; Hunter 1988, Fjeldså 1993, Hawkins et al. 2000), each of which, like the Titicaca grebe, was endemic to a single waterbody. The Titicaca grebe is thought to be potentially more vulnerable to anthropogenetic disturbance because it is flightless and entirely aquatic; it cannot walk on dry land without its legs buckling under its own weight (Loza Del Carpio 2019). In addition to being endemic and vulnerable to anthropogenic pressures, the Titicaca grebe is also of high conservation priority because it is considered an important indicator species for the health of the wider Lake Titicaca ecosystem (Pulido Capurro 2018, Medrano Sánchez et al. 2019).

Population surveys conducted in the late twentieth and early twenty-first century suggested that the Titicaca grebe was experiencing a rapid decline in population (i.e., 70% decline between the 1970s and early 2000s; Engblom et al. 2001, Konter 2006, Martinez et al. 2006). Various factors have been suggested as potential causes of the decline, including pollution (Ibarguchi 2014), changes in the Titicaca ecosystem caused by the introduction of salmonids and pejerrey in the mid-twentieth century (Villwock 2001, Martinez et al. 2006), habitat loss (Villar et al. 2023), and by-catch (Engblom et al. 2001, Martinez et al. 2006).

Of these, only one, habitat loss, has been ruled out as a likely cause of population decline (Villar et al. 2023). Bycatch is considered by most to be the main cause of observed declines in the grebe population and is the focus of the limited conservation work offered to this species (Medrano Sánchez et al. 2019, Servicio Nacional de Áreas Naturales Protegidas por el Estado 2020) because the decline in grebe numbers coincided with a rapid increase in the size and the modernization of the fishing fleets on Lake Titicaca (Laba 1979, Orlove 2002). The last surveys of Titicaca grebe populations were carried out >20 years ago, before the collapse of native and introduced fisheries (Sagárnaga 2018, Escobar la Cruz 2021). This has caused a reduction in fishery catch in the lake, exacerbating conflict between local people and the grebe (Quispe et al. 2024; Villar et al. 2024*b*, *c*), and encouraged a conversion towards pisciculture, which in other regions has been accompanied by declines in bycatch numbers (Barrett et al. 2019, Burr et al. 2023).

We present the results of a population census of the Titicaca grebe to provide up-to-date information for conservationists and wildlife managers in the Lake Titicaca region. We also determined habitat occupancy related to the role of protected areas in this species' conservation and management. This is therefore primarily a descriptive paper, meant to provide the groundwork for conservation and management decisions in the Lake Titicaca region, and to provide a basis for future work on the ecology of the Titicaca grebe.

STUDY AREA

Lake Titicaca (15°49′30″S, 69°19′30″W) is located in the central Andes of South America and is shared between Peru and Bolivia. In Peru the lake is in Puno Province, and in Bolivia it is located in La Paz Province. The lake has a surface altitude of 3,814 m (Wirrmann 1992), though this can fluctuate within and between years, making it the highest navigable lake on Earth. The lake has a total surface area of 8,300 km^2, split between Peru and Bolivia. Artisanal fishing is common on Lake Titicaca, and there is extensive tourist trade in Puno Bay, especially between the city of Puno and the Uro islands. More recently, pisciculture has come to dominate many of the coastal regions of the lake. The climate of the Altiplano is moderated by the presence of Lake Titicaca, making the region around the lake warmer than other Andean regions of comparable altitude (Roche et al. 1992). Temperatures normally

fluctuate between close to 0°C at night, and ≤10°C in the day. There are 2 primary seasons in the region, a rainy season, which usually runs from September to March, and a dry season, which usually runs from March to September. In recent years the rainy season has begun later and been shorter, leading to prolonged droughts. The vertebrate fauna primarily consists of birds, especially the Andean coot (*Fulica ardesiaca*) and the Andean gull (*Chroicocephalus serranus*), and fish, mainly of the genus *Orestias* and invasive salmonids and Argentine pejerrey (*Odonesthes bonariensis*). The endemic Titicaca water frog (*Telmatobius coleus*) is also a conservation priority (Quispe et al. 2024). In addition to Lake Titicaca, we surveyed several nearby waterbodies where the Titicaca grebe was suspected of being present, including Lake Arapa and Lake Umayo; we did not include these sites in analysis because of a lack of information on relevant environmental covariates for these outlying populations. This does not mean that these outlying populations are not important to this species (Konter 2006). We conducted surveys between March and September 2022.

METHODS

On the Bolivian side, most work was carried out from the lake shore, while on the Peruvian side we largely used transects across the lake. Surveys differed by country because of differences in local circumstances. We used a mixture of transect and point surveys depending on the time and equipment available at each site, and the weather conditions when we visited each site. We surveyed between March and September 2022 on the Peruvian and Bolivian sides of Lake Titicaca. We focused on areas where we already suspected grebe populations to exist based on the previous work of Martinez et al. (2006) and Villar et al. (2023; Figure 1). On the Peruvian side of the border, authors DAV and ERGT were present for all surveys, and on the Bolivian side of the border DAV and ACPC were present for all surveys. We attempted to visit all sites ≥2 times during the field season, which was not always possible.

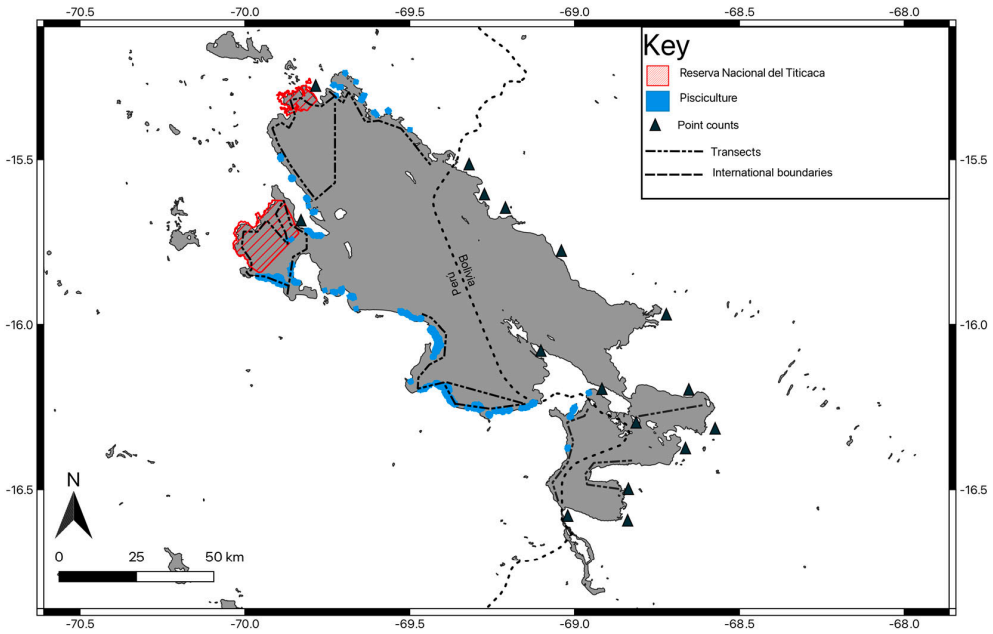


FIGURE 1 Lake Titicaca, Peru and Bolivia, with transects and point counts of population surveys conducted between March and August 2022 for the Titicaca grebe.

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Environmental covariates

Variable selection was based on knowledge of Titicaca grebe ecology, the suspected anthropogenic pressures it faces, and variables important in estimating the populations of other grebe species. We obtained the percent of area covered by totora from Villar et al. (2023). We obtained water depth from an internal bathymetric map prepared by the Autoridad Binacional Autónoma del Sistema Hídrico del Lago Titicaca. We calculated distance from shore, distance from protected areas, and distance from population centers using data from various sources (Messager et al. 2016, Lloyd et al. 2017, Servicio Nacional de Áreas Naturales Protegidas por el Estado 2022) and calculated distances in the QGIS software. We obtained data on the presence of aquaculture from satellite imagery. Bycatch is thought to be a major anthropogenic pressure on the Titicaca grebe (Engblom et al. 2001, Martinez et al. 2006, Quispe et al. 2024), but unlike other relevant variables cannot be determined from remote sensing data. Thus, we counted the number of nets and pisciculture cages in each transect or point survey, including abandoned nets whose effect on bycatch is often ignored (Laist 1996). Pisciculture cages are rarely moved and exist almost exclusively on the Peruvian side of Lake Titicaca. They are therefore included as a category of their own. Fishing intensity, and thus number of nets, is much more variable, and can vary day-to-day depending on the availability of fish and idiosyncrasies of individual fishers (Orlove 2002). To map the probability of fisheries occurring in any given pixel, we used maximum entropy distribution models (Phillips et al. 2006). Fish nets can be easily observed because of the floating plastic bottles used by fishermen to mark their locations, and we counted them when we counted birds in the transects. We then verified these models on the ground by visiting locations where it was estimated that fisheries were likely to occur based on the model but had not been visited previously. More information on modeling fisheries using distribution models, and bycatch estimates of these models, can be found in Villar et al. (2024*d*). We carried out geographic analysis at a resolution of 1 km × 1 km.

Modeling

For the habitat suitability modeling, we used maximum entropy (MaxEnt) modeling (Phillips et al. 2006). This is a presence-only habitat suitability modeling approach that is more accurate than other habitat suitability models (Elith et al. 2006, Phillips et al. 2006, Valavi et al. 2022). To control for potential geographic bias in surveyed areas, we created bias files based on survey areas using Gaussian kernel density modeling (Elith et al. 2010), as implemented in the MaxEnt software. To prevent model overfitting, we only included 1 presence point per pixel, and then applied spatial thinning to presence points to ensure that they were always ≥500 m from each other. We saved 25% of presence points for model validation and used 10,000 random pseudo-absence points (Barbet-Massin et al. 2012). We evaluated MaxEnt models using area under the curve (AUC; Jiménez-Valverde 2012).

While MaxEnt is a commonly used and robust method for estimating species distributions, it assumes that there is a perfect chance of detecting a species if it is present at a site and that presence points are partially homogenous. Neither of these assumptions are likely to be true, especially for rare and poorly studied species (Syfert et al. 2014, Sutton et al. 2023), potentially leading to unreliable range and abundance estimates (De Castro Pena et al. 2014). To account for these shortcomings, various methodologies have been developed (e.g., occupancy modeling; MacKenzie et al. 2018). Occupancy modeling incorporates known absences from sites that have been surveyed multiple times, including environmental covariates, to develop habitat suitability models. It has been used previously to estimate potential range and abundances (Calderón et al. 2022, Fuller et al. 2022). We obtained absence points from transects where we did not observe grebes. We used a single-season occupancy model, and then used the same logic and method as used in the MaxEnt model to estimate population abundance. We used the same environmental covariates as we had used in the maximum entropy modeling. The detection covariates were the start time of the survey, the day of the survey, the duration in minutes of the survey, the survey team involved, and the length of the transect, with zero for point counts. We scaled non-factorial variables (i.e., all except survey team

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and cage presence). We conducted occupancy modeling using the spOccupancy package (Doser et al. 2022) in R version 4.30 (R Core Team 2023). Unlike other R libraries used in occupancy modeling, spOccupancy allowed us to create spatially explicit occupancy models, which can help correct for issues related to spatial autocorrelation and spatial sampling bias. As spOccupancy uses a Bayesian approach, we validated occupancy models using Bayesian *P*-values and the Freeman-Tukey test statistic (Freeman and Tukey 1950), with models considered to fit the data well if their Bayesian *P*-values were between 0.1 and 0.9 (Hobbs and Hooten 2015).

The MaxEnt and occupancy models provide a continuous output estimating the likelihood of grebe presence or absence or abundance in each pixel. To convert these continuous maps into a binary map that could be used to estimate abundances, we used the lowest presence threshold method (Phillips et al. 2006). This assumes that the point with the lowest probability of hosting grebes but where grebes are present is the minimum threshold for habitat suitability for the grebe. We converted estimates from the probabilistic maps to binary maps using a custom function originally written by C. B. Morrow, but which was not published as part of an R package. We also used a more conservative estimate of converting the continuous maps into binary maps using an arbitrary 50% chance of grebe presence according to the model.

Comparing model results

We used 95% confidence intervals when estimating grebe abundance when comparing the different models. For species distribution models, following the logic of Mladenoff and Sickley (1998) and Long et al. (2008), we obtained population size for each year by multiplying the area of predicted extent by the average population density found across surveyed sites where we observed grebes. We used 2 distinct sources for the population density of the Titicaca grebe. The first is the reported population density from Martinez et al. (2006), which was an average population density of 6.1 individuals/km^2, with a 95% confidence interval of 2.06–10.15 individuals/km^2. This study had the advantage that set regions with known areas were surveyed, giving more accurate data on population densities. We also estimated the population densities from our surveys, using the effective range of our binoculars. From the experience of authors, accurate species identification of Titicaca grebes is not possible beyond 500 m using 8 × 42 magnification binoculars. We therefore considered the area surveyed to be 500 m from the observer for point counts, and 500 m in either direction, totaling 1,000 m, for transects. We therefore calculated density from point counts assuming a circle with a 500-m radius. We used the standard deviations of the grebe's population of each area we counted to estimate uncertainty. We compared geographic distribution of the occupancy and habitat suitability models using Godsoe's expectation of shared presence, Warren's *I*, itself a derivative of Hellinger's distance, and Schoener's *D* (Schoener 1970, Warren et al. 2008, Godsoe 2014, Jha and Nameer 2022). Each provides an output ranging from zero, indicating no overlap, to 1, indicating perfect overlap (Rödder and Engler (2011). We made plots in R using ggplot2 (Wickham 2016), and maps in QGIS.

RESULTS

We counted 6,118 grebes in 36 point counts and 115 transects, including repeated surveys. Of these, 16 point counts and 3 transects were in Bolivia, and 20 point counts and 112 transects were in Peru. We estimated an average population density of 10.68 individuals/km^2 (6.46–14.90). Grebes were primarily observed near the coast, and in shallow waters. Grebes were found in a variety of environments, ranging from locations where >90% of the pixel was totora wetland to locations in open water, and from areas with <1 m of surface depth to locations where the water depth was >100 m (Table 1). The MaxEnt model had an AUC of 0.893, indicating high accuracy. The contributions of each individual factor to the model were, in descending order of importance, fishing intensity (68.6%), distance from a protected area (10.8%), distance from pisciculture cages (9.1%), totora cover (5.5%), water

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TABLE 1 Extreme values for environmental covariates used to construct distribution models of the Titicaca grebe in pixels where we observed the Titicaca grebe in Lake Titicaca, Peru and Bolivia, during transect and point counts conducted in March–August 2022, with binary environmental covariates excluded.

	Max. value	Min. value	Max. value coordinates	Min. value coordinates
Totora extent (% of pixel)	91.58	0.00	−15.485, −69.364	−15.880, −69.879
Distance from Reserva Nacional del Titicaca (km)	150	0 (inside protected area)	−16.286, −68.606	−15.830, −69.980
Distance from shore (km)	4	<1	−15.362, −69.816	−15.860, −69.941
Distance from settlement (km)	5	<1	−15.409, 69.856	−15.784, −69.803
Distance from pisciculture (km)	49	<1	−15.761, −69.073	−16.060, −69.413
Fishing intensity (number of nets)	114	0	−15.722, −69.792	−15.574, −69.295
Water depth (m)	103	<1	−16.583, −68.864	−15.485, −69.364

depth (3.7%), distance from a settlement (1.2%), distance from the shore (1.1%), and presence of pisciculture cages (0.0%). Approximately 1,081 km^2 had a ≥50% chance of harboring the grebe (Figure 2), and using the 50% suitability threshold we estimated 11,545 (6,988–16,105) grebes from our population density estimates and 6,954 (2,228–10,972) grebes from the population estimates from Martinez et al. (2006; Figure 3). Using the minimum training threshold, 3,747 km^2 of area was suitable for the Titicaca grebe, which resulted in a population average of 22,856 (7,722–38,033) grebes using the density estimates of Martinez et al. (2006) and 40,018 (24,223–55,825) grebes using our density estimates. Areas with higher fishing intensity, closer to protected areas, with totora cover, that were shallower, between 1 km and 5 km from settlements, and between 2 km and 10 km from shore all were more likely to harbor suitable habitat for the Titicaca grebe.

The occupancy model was accurate in estimating grebe locations, with a Bayesian *P*-value of 0.4907. The spOccupancy package does not include the percentage contribution of each explanatory variable in the model outcome, but it does provide the Bayesian credible interval (BCI) of the effect of each variable on modeled grebe habitat suitability. The 95% BCI crossed the zero-effect size boundary for all variables. The 75% confidence limits for distance from the shore and fishing intensity did not cross zero (Figure 4), suggesting that these were real effects. The occupancy model had 4,072 km^2 with a ≥50% chance of harboring a grebe population (Figure 3), and using the 50% suitability threshold we estimated a population of 43,488 (26,324–60,667) grebes based on our estimated population densities, and a population of 24,839 (8,391–41,332) grebes based on the population densities reported in Martinez et al. (2006). Using the minimum training threshold, 4,182 km^2 of area suitable for the Titicaca grebe was available, which resulted in an estimated population average of 44,664 (27,035–62,306) grebes using our density estimates and 25,510 (8,618–42,449) grebes using the density estimates of Martinez et al. (2006). The occupancy model and the maximum entropy model had a Warren's *I* of 0.684, a Schoener's *D* of 0.442, and a Godsoe's expectation of shared presence of 0.317, indicating a moderate overlap between the results of these models.

DISCUSSION

We have confidence in the results of maximum entropy and occupancy modeling although they reported very different results regarding the grebe's geographic range. From unpublished reports of the Peruvian government detailing the location of grebe populations in Peru (C. A. Loza and R. Rojas, 2003, Instituto Nacional de Recursos Naturales, unpublished report; E. Gutiérrez, 2004, Instituto de Investigaciones Biológicas y Desarrollo Sostenible,

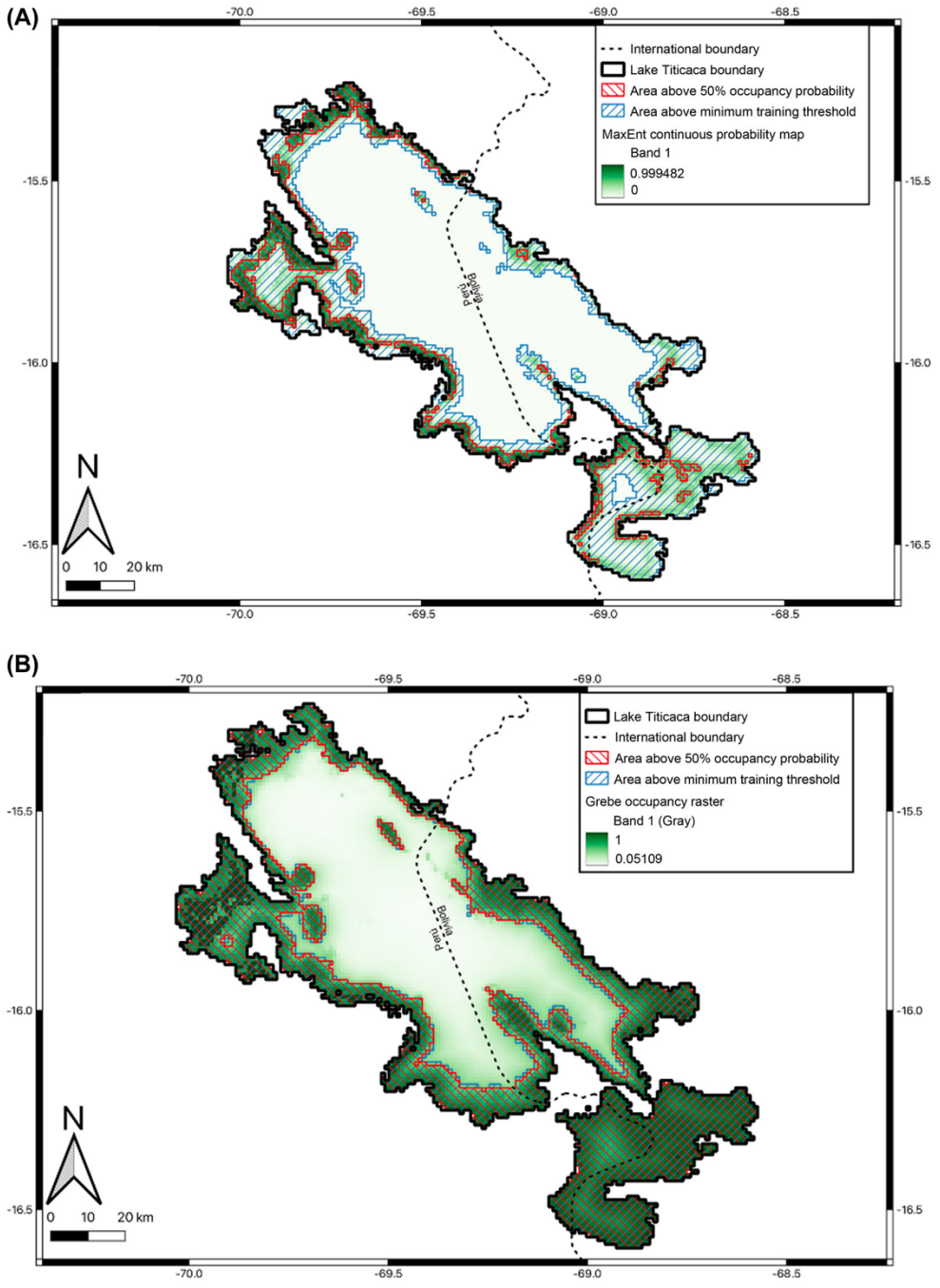


FIGURE 2 Map of the predicted habitat suitability for the Titicaca grebe in Lake Titicaca, Peru and Bolivia, using A) MaxEnt and B) occupancy analysis following surveys in 2022.

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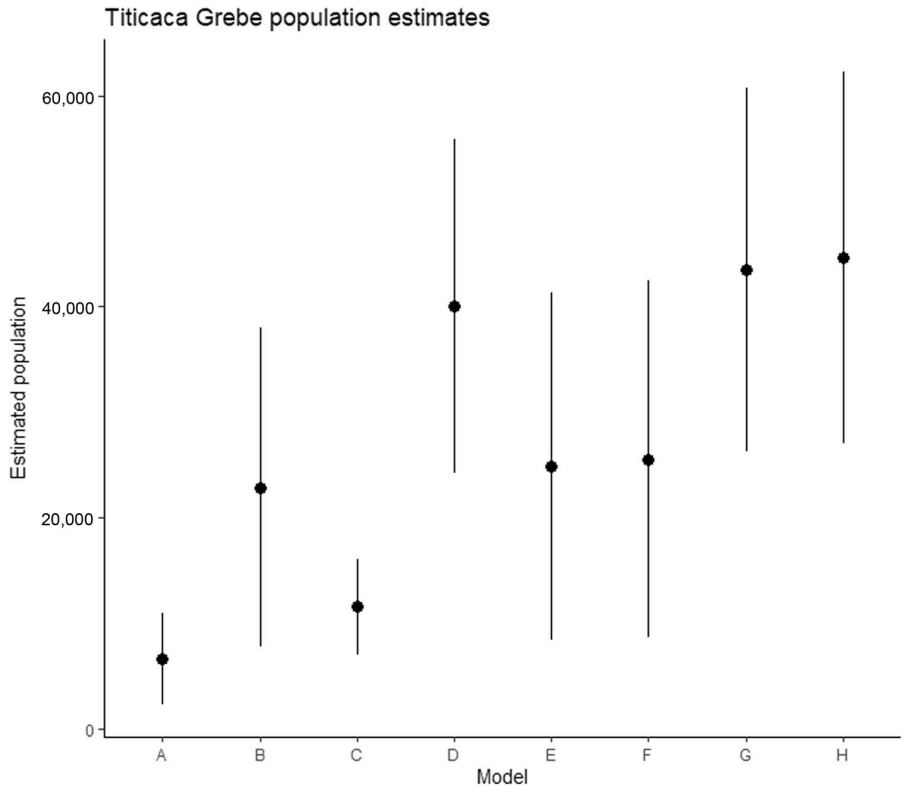


FIGURE 3 Population estimates of the Titicaca grebe, with 95% confidence intervals, in Lake Titicaca, Peru and Bolivia, 2022. A) MaxEnt model using Martinez et al. (2006) population density and 50% suitability threshold, B) MaxEnt model using Martinez et al. (2006) population density and minimum training threshold, C) MaxEnt model using this study's estimated population density and 50% suitability threshold, D) MaxEnt model using this study's estimated population density and minimum training threshold, E) occupancy model using Martinez et al. (2006) population density and 50% suitability threshold, F) occupancy model using Martinez et al. (2006) population density and minimum training threshold, G) occupancy model using this study's estimated population density and 50% suitability threshold, and H) occupancy model using this study's estimated population density and minimum training threshold.

unpublished report), and from previously published known sites across Lake Titicaca of grebe populations (Martinez et al. 2006), we suggest that the occupancy model provided a more accurate view of the Titicaca grebe's range. While there is no statistically significant difference between the population estimates stemming from our counts and those from density estimates from Martinez et al. (2006), we suspect that the latter are more likely to reflect the true population range of this species. This is not because we distrust our abundance counts, but because estimating population from counts made over open water has inherent difficulties that make estimating area covered more difficult than the methods of Martinez et al. (2006); their study began with an area of known size and they counted within it. Future studies, with more accurate ways of measuring the distance of individuals from observers than dead reckoning, could apply a distance sampling curve (Buckland et al. 2001) to gain a more accurate idea of the population densities of the Titicaca grebe. The occupancy model confirms that the Titicaca grebe is primarily a coastal species, and that it is associated with the areas with aquatic vegetation, such as in clumps of totora or amongst floating carpets of Eurasian watermilfoil (*Myriophyllum* spp.).

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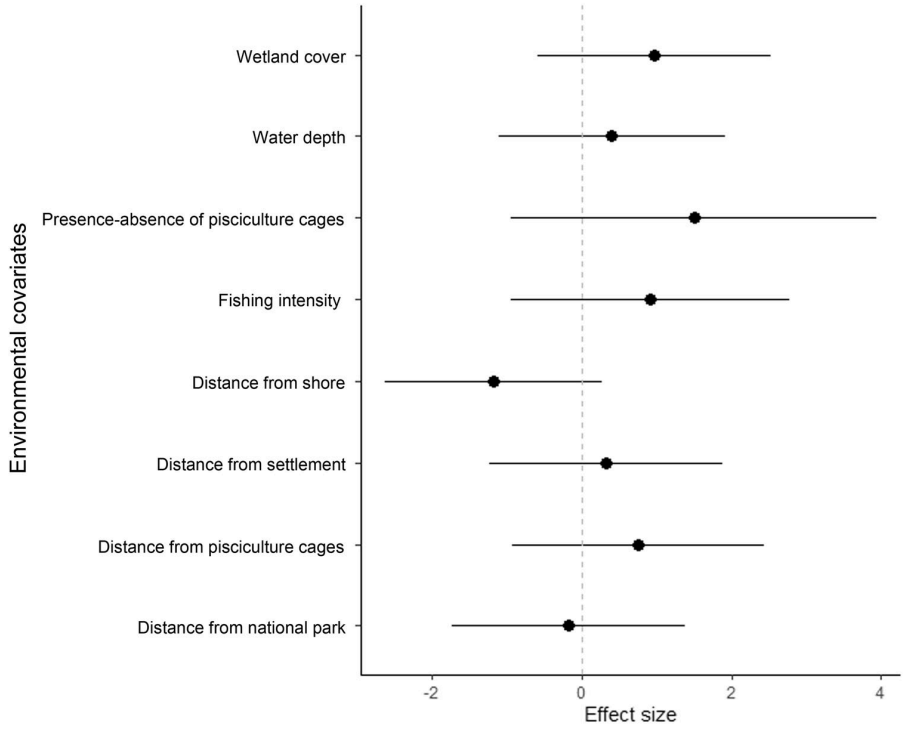


FIGURE 4 Effect coefficients and 95% Bayesian credible intervals (BCI) of each environmental covariate used in the Bayesian occupancy model to assess modeled Titicaca grebe habitat suitability for regions of Lake Titicaca, Peru and Bolivia, 2022. No variable had a BCI of 95% that did not cross zero. Fishing intensity and distance from shore have 75% BCIs that do not cross zero.

The Titicaca grebe is listed as having between 250 and 999 individuals by BirdLife International (BirdLife International 2024*b*). There was already reason to believe that this was a severe underestimate of the species' population, as both demographic modeling (Callaghan et al. 2021) and estimates on the basis of available breeding habitat (Villar et al. 2023) had placed the population of the Titicaca grebe between 5,000 and 10,000 individuals. However, our study suggests a significantly greater population than that previously estimated. There is no historical baseline of Titicaca grebe populations prior to the opening of commercial fisheries with which to compare these estimates, but some early ornithological writings on the region did describe the Titicaca grebe as the most common bird species in Lake Titicaca (Sclater and Salvin 1869). Our estimates represent a significant increase from population figures reported 20 years ago (Engblom et al. 2001, Martinez et al. 2006) and are closer to population estimates conducted 40 years ago, when that number of grebes could be found within Puno Bay alone (Fjeldså 1981). As there has been no concentrated grebe population monitoring effort in the intervening 2 decades, we cannot pinpoint the exact cause of this increased population, although an increase in available breeding area may be responsible (Villar et al. 2023). A likely alternative, however, is a decline in fisheries bycatch across Lake Titicaca.

Fisheries bycatch was the suspected cause of population declines in the early 2000s (Engblom et al. 2001, Martinez et al. 2006). Hostility from fishers towards the grebe remains a significant barrier to community conservation efforts in the region (Quispe et al. 2023, Villar et al. 2024*b*), and anti-bycatch efforts are likely required to help preserve this species' population over the long term. However, there has been a decline in many traditional

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economic activities around Lake Titicaca (Villar et al. 2024*a*), including fisheries. Many parts of the rural Altiplano around Lake Titicaca are depopulated of young people, most of whom move to cities or mines in search of greater economic opportunity (D. A. Villar, University of Oxford, personal observation). Furthermore, many of those who used to fish have moved to other economic activities. Over a decade ago, anthropologists noted that the Uro, an ethnic group who historically lived almost exclusively by fishing and hunting game, were moving increasingly into tourism (Kent 2006, 2008, 2013). This transition is now almost complete, and very few Uros around Puno Bay do any fishing (D. A. Villar, personal observation). Furthermore, many fishers have transitioned from fishing to fish farming, especially as the wild fish of Lake Titicaca have been overfished.

While fish farming has not always proven to be a relief for wild fish populations, as was once expected (Diana 2009, Barrett et al. 2019, Longo et al. 2019), it is likely that its expansion has benefitted the Titicaca grebe. Titicaca grebes are not caught in fish farm nets, possibly because their ecology (Martin and Crawford 2015) makes them more visually sensitive to the thick black net material used for fish farms compared with the near-invisible monofilament nets used for fishing, and most fishers who transition to pisciculture cease fishing (D. A. Villar, personal observation). The presence of these changes to pisciculture does not seem to provide suitable habitat for the grebe. What remains to be seen, is whether trout escaping from these fish farms have deleterious effects on the Titicaca grebe, and on the wider Lake Titicaca ecosystem, as did their intentional introduction in the twentieth century (Lauzanne et al. 1992, Hall and Mills 2000, Vila et al. 2007). However, even with this potential negative impact of escaped invasive salmonids, we suspect that the expansion of fish farms has been a net boon to the Titicaca grebe.

The Reserva Nacional del Titicaca has some of the best situated territory for Titicaca grebe populations in its entire range. This follows previous work that found that the largest contiguous area of suitable breeding habitat for the Titicaca grebe is in the Reserva Nacional del Titicaca in Puno Bay (Villar et al. 2023). This suggests that the Reserva is well placed, and its proper funding is important for the conservation of this species. However, it does not appear that there is a significant impact of being in the park on grebe habitat suitability. This suggests that the Reserva is acting as a refuge because of where it is rather than what it does. The Reserva Nacional del Titicaca is underfunded and understaffed, and we hope that this paper can help highlight the global importance of this protected area, and encourage greater investment in it by the Peruvian government.

Although we suggest that the Titicaca grebe population is healthy in Lake Titicaca, we did not assess the state of outlying populations. Already some regions that were known to have populations of the species, such as Lake Poopó (Martinez et al. 2006) and the Laka Jahuira River (Konter 2006) have dried up (Torres-Batlló et al. 2019, Perreault 2020). It is likely that many other peripheral populations have been lost with the droughts that have plagued the Altiplano since 2022. Other areas with grebe populations, such as Lake Umayo and Lake Arapa, have not dried up, but we excluded these sites from this study because of the lack of available environmental information required to construct species distribution models. We surveyed some of these sites, and provide information on their grebe populations (available at https://datadryad.org/stash/share/Y26l5CPzSMNuep1AxqNUs0wjhCGqwSUYRE9mm39IUPc). Further research is required to study the biodiversity of smaller lakes and rivers of the Altiplano, for the conservation of the Titicaca grebe and to document these ecosystems before they are all lost to drought and global warming.

Despite this species having a significantly higher population than previously estimated, we do not recommend a change to its listing by the IUCN. This is for 3 reasons. First, both this work and previous studies have shown that the Titicaca grebe is liable to significant fluctuations in population (Engblom et al. 2001, Martinez et al. 2006). The high population reported in this study could be a snapshot of a good year, and the authors have reason to believe that the grebe population has already declined since these surveys took place owing to the severe drought experienced by the Altiplano region in 2023. Second, the Titicaca grebe remains endemic to a small area. While being endemic to a small area should not itself cause a species to be endangered, those with smaller spatial ranges are more vulnerable to extinction (Stattersfield et al. 1998, Manne et al. 1999, Gaston and Fuller 2009). While the Titicaca grebe can colonize newly suitable areas quickly (Fjeldså 1981, Konter 2006), it is currently experiencing significant pressures on its primary environment. Specifically, water levels in Lake Titicaca have reached the lowest recorded in over 25 years (Servicio Nacional de Meteorología e Hidrología del Perú 2023). Other major lakes in the region, such as Lake Poopó, have

already dried out. While we do not expect Lake Titicaca to disappear entirely, its significant shrinking is foreseeable, which could cause the extinction of the Titicaca grebe. Third, the Titicaca grebe is a high-altitude species, with a limited altitudinal range, as far as we know. Global warming is a risk for all high-altitude species (Thomas et al. 2004), but those with narrow altitudinal ranges are especially vulnerable to its effects (Freeman et al. 2018). For all of these reasons, we recommend that the Titicaca grebe continue to be considered endangered.

The state of the Titicaca grebe as presented in this study suggests that it may offer a rare sign of hope for endangered members of this family in South America. Recent surveys in Lake Junin, in central Peru, have shown declines in populations of the endemic Junin grebe (*Podiceps taczanowskii*) from several tens of thousands in the 1930s to only a few hundred individuals in the 2010s (Dinesen et al. 2019), while work on the hooded grebe (*Podiceps gallardoi*) in Patagonia shows that populations there have declined by over 80% in the last 25 years (Roesler et al. 2012). These species are suffering from similar anthropogenic pressures as the Titicaca grebe, such as death by fisheries bycatch (G. Engblom, Kolibri Expeditions, personal communication), invasive salmonids (Lancelotti et al. 2017), pollution from mining (Dinesen et al. 2019), and climate change (Lancelotti et al. 2020). Comparative work on these grebe populations and their ecologies is needed to explain why the Titicaca grebe population has seemingly recovered from a nadir in the early 2000s, while these other grebe species have continued to decline.

CONSERVATION IMPLICATIONS

The significant disparities between the estimated population estimates in this study and those of the IUCN suggest that a lack of continual monitoring of this species had led to inaccurate information entering global conservation databases. This should act as a warning for population estimates of other poorly monitored species in global conservation databases, such as those of the IUCN. The Reserva Nacional del Titicaca is situated in some of the most suitable environment for the Titicaca grebe in its entire range, and the Reserva ought to be given more resources from the central Peruvian government, which controls its budget, to function as effectively as it could as a protected area. The significant differences in population and range estimates between models suggest that researchers working with other species test various models to estimate range and populations, and that comparisons of population and range estimates derived by different methods ought to be viewed with caution.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

We obtained necessary research permits to conduct this work from both the Peruvian (N° 004- 2022-SERNANP-RNT-J) and Bolivian governments (MNHN°020/202), and received permission from all local communities where work was conducted. Local authorities no not issue formal research permits but rather permitted researchers to conduct research after discussions with them.

DATA AVAILABILITY STATEMENT

The data used in this paper can be accessed at https://datadryad.org/stash/share/Y26I5CPzSMNuep1AxqNUs0wjhCGqwSUYRE9mm39IUPc.

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The data used in this chapter can be found in appendix B

4

Indigenous–Wildlife Conflict and Coexistence in the Altiplano

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Indigenous–Wildlife Conflict and Coexistence in the Altiplano

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Abstract

Understanding the drivers of conflict and coexistence in human–wildlife relations are critical to conservation. This study sought to understand th varying attitudes of local indigenous people towards wildlife, focusing on the Titicaca Grebe (*Rollandia microptera*), an endangered endemic species found in Lake Titicaca and surrounding waters in the Altiplano of Peru and Bolivia. We used an ethnobiology approach to understand which demographic, sociocultural, and economic factors influenced (a) attitudes and local ecological knowledge (LEK) towards the grebe and (2) their effects on Indigenous–wildlife conflict or coexistence. We used a qualitative, semi-structured questionnaire to interview 221 individuals over six months in villages surrounding Lake Titicaca. Participants primarily consisted of locals from the Aymara, Quechan, and Uro Indigenous groups. We found that most individuals expressed apathy towards the grebe, with a significant minority being hostile towards it. Hostility was concentrated amongst fishers and was driven by economic concerns. Knowledge of the grebe was low in the general population, but higher amongst fishers. There was, however, widespread willingness to conserve the grebe amongst the general population, particularly when informed that the grebe is endemic to the Altiplano. This small environmental education intervention suggested increased positive attitudes and a willingness to conserve the grebe. Non-homogenous perspectives towards the grebe were held within and between indigenous groups, suggesting the need for future research into intra-indigenous group dynamics in indigenous–wildlife relations. Future conservation work on the Titicaca Grebe should focus on reducing grebe-fisher conflict, both real and perceived, and on educating people on the grebe's endemic status.

Keywords

ethno-ornithology, conservation social science, local ecological knowledge, human–wildlife conflict, conservation attitudes, Altiplano, indigenous

Introduction

In recent decades, there has been increasing emphasis on the importance of understanding social-ecological systems within conservation biology (Dayer et al. 2020; Psuty and Całkiewicz 2021). Core to this shift has been the integration of ethnobiology into conservation research (O'Neill et al. 2017; Turner, Cuerrier and Joseph 2022). Ethnobiology is the study of the interactions between humans and nature from an anthropological and biological perspective and can act as a bridge between social and natural scientists (Anderson et al. 2011). The practice of ethnobiology often involves working with indigenous people in the management of ecosystems and integrating indigenous ways of understanding the natural world into ecological management decisions (Turner, Cuerrier and Joseph 2022; Ulicsni et al. 2019). This is a valuable pluralistic approach to social-ecological systems research due to its inclusion of different disciplines without sacrificing the respective norms of each (Thomsen 2022).

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Understanding local ecological knowledge (LEK) drivers and attitudes towards wildlife are of interest because they have conservation implications (Heberlein 2012; Hopper et al. 2019; Schultz 2011). Previous work shows that while more information about species can increase the conservation ethos locally (Ardoin, Bowers and Gaillard 2020; Kamudu, Rollnick and Nyamupangedengu 2022), this is not always the case (Ardoin, Bowers and Gaillard 2020). LEK is an important supplement to Western scientific knowledge of the behaviour and distribution of species that have not received significant scientific attention (Gilchrist, Mallory and Merkel 2005; Joa, Winkel and Primmer 2018). This natural history knowledge can, in turn, be useful to conservation (Joa, Winkel and Primmer 2018), especially when considered in conservation planning and management and in collaboration with local and indigenous peoples.

LEK is not static; instead, it changes as people's relationship with their natural environment changes. There is sometimes a tendency to essentialise LEK, especially indigenous LEK, as something intrinsic to the existence of a group, and place it out of time and context (Clarke 2023). However, we know from studies both of indigenous groups and non-indigenous groups that what LEK exists, and how it is used, tends to change, even as the people are not aware of it changing. This can be termed 'shifting-baseline syndrome', a phenomenon which is primarily associated with ecology, where people assume that the conditions under which they grew up are the natural condition of an ecosystem (Pauly 1995). However, shifting-baseline syndromes can also apply to the state of human societies, with people assuming the norms and knowledge of the society which they grew up in are a trans-historic norm, from which change deviates. For LEK, this can mean that changes in ecosystems (Kai et al. 2014; Turvey, Bryant and McClune 2018), economic changes in how cultures operate and interact with their natural environment (Paredes and Hopkins 2018; Villar et al. 2024), or a mixture of both can change LEK (Mitchell 2015).

Knowledge of the drivers of attitudes towards wildlife is especially important for redressing human–wildlife conflict (McMahon et al. 2023). Conflicts can emerge in various degrees of severity, but the most common are 'disputes', which are centred around a material issue (Cusack et al. 2021). That disputes revolve around a potentially measurable issue does not mean that perception does not matter in addressing them – often local stakeholders will have different perspectives on the degree and severity of disputes than exogenous scientists (Duriez et al. 2019; Inskip and Zimmermann 2009). These different perspectives may have underlying cultural and economic causes, which need to be understood before implementing conservation programmes (Hodgson et al. 2019; Lambertucci et al. 2021). By understanding the drivers of human–wildlife conflict, coexistence can be reframed as a pathway for people to accept or even actively support conservation measures (Carss 2022; Douglas and Veríssimo 2013). However, knowledge of such cultural drivers can only come from studying cultural and biological contexts (Torrents-Ticó et al. 2023), which the ethnobiological approach provides.

While human–wildlife conflict exists to some degree in all societies, indigenous societies often exhibit high degrees of coexistence with wildlife that many Westerners perceive as 'problematic' (Baynes-Rock 2013; Jolly et al. 2022). Indigenous–wildlife coexistence is thought to stem from cultural norms that have coevolved with wildlife in a specific area, and many issues of global human–wildlife conflict occur when this knowledge has been lost (Pettersson et al. 2021). The Andes especially has a widely shared cultural cosmovision, which respects the earth as a sacred mother, or Pachamama, and encourages taking care of Her (Mamani-Bernabé 2015; Sarmiento 2010). This Andean-Cosmovision appears to have environmental implications, as those who care more about it practice more traditional agricultural techniques (Rist, Burgoa and Wiesmann 2003), and are more willing to participate in habitat restoration (Hartman, Cleveland and Chadwick 2016). However, this view of indigenous–wildlife coexistence has been criticised by some for falling into the stereotype of the 'ecologically noble savage', pointing out that not all indigenous groups act or think as proto-environmentalists (Alvard 1993; Redford 1991). Without wishing to revive that acrimonious debate (Raymond 2007), we study how human–wildlife conflict and coexistence can occur simultaneously amongst indigenous and local peoples, between different indigenous groups in the same area (i.e., Aymara and Uro), and what drives this concurrent conflict and coexistence.

This article focuses on a subset of ethno-biology, ethno-ornithology, for its examination of the Titicaca Grebe and its relationship with local Indigenous peoples. Ethno-ornithology moves beyond simply studying birds and their presence in human cultures, but rather focuses on the deep interdependent relationships between humans and birds. These deep bird–human relations are omnipresent in all societies globally but often acutely represented in many Indigenous societies (see Barman et al. 2020; Tidemann and Gosler 2012). The Titicaca Grebe is an endangered flightless endemic found in Lake Titicaca and surrounding lakes and rivers (Fjeldså 1981, 2004; Fjeldså and Krabbe, 1990; Martinez, Aranibar and Gutierrez 2006; Villar et al. 2023). Although it was historically common within this range (Fjeldså 1981), population surveys during the late 20th and early 21st century showed that its population declined by up to 70% between 1970 and 2000 (Engblom et al. 2001). The drivers of this decline are unknown, but the main suspect is fisheries bycatch caused by increases in fishing and modernisation of fishing gear (Martinez, Aranibar and Gutierrez 2006). This could have reduced the grebe population both by increasing mortality through bycatch, and by reducing the amount of the grebe's main prey, fish (Fjeldså 1981), in the lake. Fishing has existed in Lake Titicaca for millennia but was historically uncommon (Miller et al. 2021; Young 1997). The introduction of Trout (*Salmo trutta*) and Pejerrey (*Odontesthes bonariensis*) caused an increase in the number of fishermen (hereon: fishers)

in the late 20th century (Everett 1973; Laba 1979; Orlove 2002), and a transition from traditional plant fibre nets to nylon monofilament nets (Orlove 2002). Grebes often get caught as bycatch in these nets. The grebe is not eaten in the region, due to its rancid taste (Loza Del Carpio 2019), and its use by traditional crafts of the region appears to be minimal (Richard and Contreras Zapata 2018). Lake Titicaca is a significantly polluted ecosystem, due to runoff from mining (Guédron et al. 2017) and untreated human wastewater (Beltrán Farfán et al. 2015). Heavy metals from mining concentrate in fish, and regular consumption of fish from the Lake Titicaca watershed has been associated with health problems in humans (De Loma et al. 2019), but it is unclear if it causes health problems for the Titicaca Grebe.

Materials and Methods

Study Sites

Lake Titicaca is shared between Peru and Bolivia, in the Central Andes. The lake has a surface elevation of 3,812 m, and surface area of approximately 8,372 km^2. It is split into two sub-lakes, Lago Menor, and Lago Mayor. The former is smaller and shallower than the latter. There are approximately 151 settlements on the shores of Lake Titicaca (Orlove, Levieil and Treviño 1992), although this can vary depending on how 'settlement' is defined. Surveys were carried out both in villages on the lakeshore and in the provincial capital city of Puno, Peru (Figure 1).

The Altiplano is a large plateau in the central Andes. It is a culturally constructed landscape (Ellenberg 1979; Young 1997) – that is, a landscape where an intensive human modification has been present for so long that it is difficult to discern what a pre-human environment was. Ethical approval was received from the Departamento de Ciencias Biologicas de la Universidad Nacional del Altiplano en Puno. Permission was obtained in each village from village authorities to conduct interviews.

Field Methods

Semi-structured interviews were conducted face-to-face between March and September 2022, with work done in Bolivia from March to June, and work in Peru from June to September. Six of the 10 authors live in the Altiplano or descend from the region, providing us etic and emic perspectives. Due to the dispersed nature of the population of the Altiplano, and the lack of reliable mechanisms to select interviewees randomly, we performed a convenience sample, meaning we interviewed those who were available and willing to be interviewed. While recognising that this is not the gold standard (Newing 2011), it has been used widely in ethnobiology (e.g., Gutiérrez Alonso et al. 2020), and is considered valid within ethnobiology (Newing 2011). The interviewers (Authors D. A. V. and A. C. P. C.) formulated a qualitative, semi-structured questionnaire (Supplemental Materials) to guide their interviews (Creswell and Creswell 2018; Thomsen et al. 2020). This included demographic questions, as well as a Likert scale of 0 to 10, with 0 being the worst (most disliked) and 10 being the best (most liked), to indicate their opinion of the grebe and their self-assessed knowledge of the grebe. Interlocutors were asked to justify both responses, giving a reason for their opinion of the grebe and asked what specific facts they knew about the grebe. Consent was gained verbally since a significant proportion of the population of the Altiplano is illiterate. Anonymised questionnaire responses are in the Supplemental Materials, but whole transcripts have not been provided.

Choosing Potential Explanatory Variables

We drew upon both the wider published literature on drivers of LEK, and upon our knowledge of the Altiplano to develop a list of potential explanatory variables. The variables we included are: Age, Education, Sex, Country, Ethnicity, Education, Residence Status, Profession Category, Fishing Involvement, Number of Languages Spoken, Primary Language Spoken at Home, and Religion.

Age and education are significant drivers of ethnobiological knowledge (Brandt et al. 2013; Mathez-Stiefel et al. 2012). This is especially the case in societies which are undergoing rapid economic and cultural change, such as the Altiplano, as these changes can lead to an erosion of ethnobiological knowledge (Gosler and Tilling 2022; Reyes-García et al. 2005, 2007). Historically, the Altiplano has not only been one of the poorest in South America, but also one of the few areas where indigenous culture dominates Spanish culture (Klarén 2000; La Barre 1948). However, there has been a rapid decrease in poverty over the past 15 years in the Altiplano, particularly in Bolivia (Webber 2016), leading to an economic divergence between the two regions of the Altiplano.

The division of labour between men and women in many societies can lead to differences in knowledge and attitudes towards the natural world (Brandt et al. 2013; Souto and Ticktin 2012). While advances have been made in support of women's rights in the Andes in recent decades, the larger Andean society still maintains strict gender roles (Pape 2008). This extends to fisheries where men tend to be fishers while their wives tend to sell fish (Orlove 2002).

Economic position can drive ethnobiological knowledge (Gruberg et al. 2022; Sogbohossou et al. 2015). This is both in terms of what profession an individual has, and what relationship with the natural environment is necessitated by said profession. Poorer individuals in traditional societies, who spend more time outdoors, often know more about the surrounding environment (Sogbohossou et al. 2015). However, some professions can lead to more hostility towards elements of wildlife, such as the hostility of farmers to predators (Duriez et al. 2019; Inskip and Zimmermann 2009), the hostility of fishermen to bycatch species that break nets (Blaber et al. 2009; Gandini and Frere 2012; Quispe et al. 2023), and to

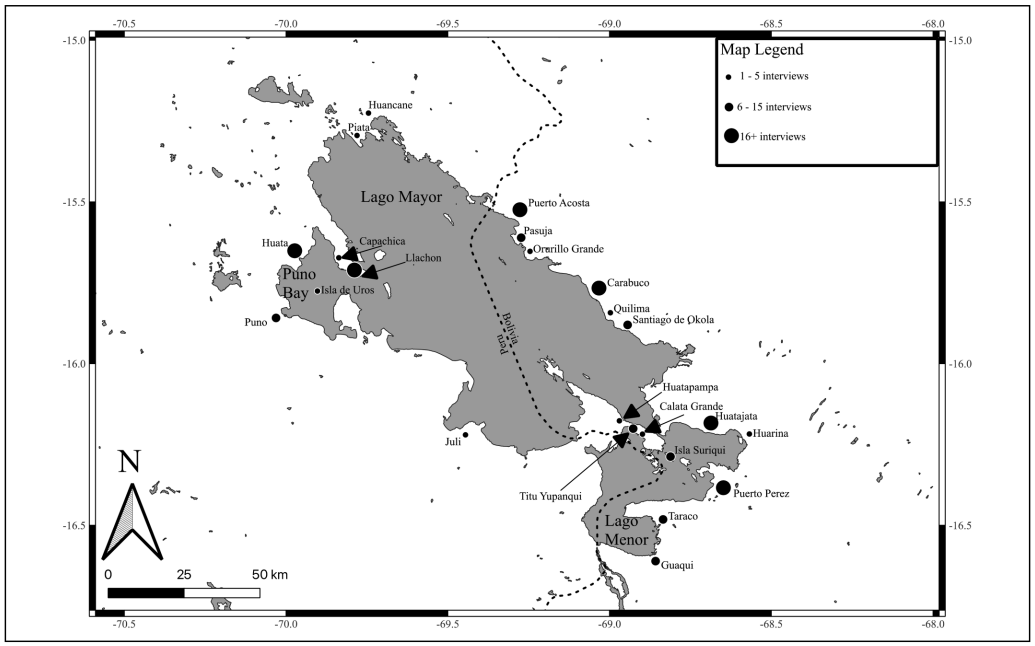


Figure 1. Map of Lake Titicaca with locations of interviews, including incomplete interviews, highlighted.

marine predators (Guerra 2019). Because of this, we included both profession category, and whether an individual was involved in fisheries, in our analysis. Profession was based on what interlocutors said was their primary economic activity. For fisheries, this meant that we included fishers in the profession category of fisheries, but included both fishers and those who sold fish in markets in the involvement of fisheries category. Most people make a distinction between *campesino*, which is an agriculturalist who primarily relies on planting, and *ganadero*, which is an agriculturalists who relies on livestock. Unskilled manual labour are profession which do not require specialised training to undertake, while skilled manual labour are jobs where some degree of apprenticeship or traineeship is expected. An example of the former would be being a bricklayer, of the latter, an electrician. Artisans were primarily those involved in making products, such as weavers. Homemakers are those who said that their primary economic activity was taking care of family life; this was primarily women. Professionals are those with white collar professions, such a schoolteachers and rural nurses. Mining primarily meant miners; we did not interview any mining engineers. Miscellaneous included all those whose profession did not fall into the above categories, and included shopkeepers, those involved in tourism, a musician, and the unemployed, amongst others.

The primary religion of the Altiplano is Catholicism (La Barre 1948; Stanish 2003), which combines elements of pre-Christian religion and Roman Catholicism. A key element of this is the worship of the Pachamama, or the mother earth (Mamani-Bernabé 2015; Sarmiento 2010). Recent decades have seen an increase of missionary activity, mostly by Evangelical Protestants (Salas 2018). These groups are often hostile to the Catholic Church's traditional laxity to 'nature worship', and Evangelicals are known to abandon local agricultural techniques that are based emically on the worship of the Pachamama (Rist, Burgoa and Wiesmann 2003).

Residents born in a community and immigrants to a community often have different levels of LEK (Souto and Ticktin 2012). Historically most people in the Altiplano would have lived near where they were born, but economic changes have caused more migration within and beyond the Altiplano.

There are often different degrees of LEK amongst different ethnic groups, even those living in the same area (O'Neill et al. 2017). The main ethnic groups of the Altiplano are the Aymara, the Quechua, and the Uro (Bouysse-Cassagne 1992; La Barre 1947; Mishkin 1947; Tschopik 1947). Of these, the Uro have historically been the most dependent on the lake (Forbes 1870; La Barre 1947, 1948; Mishkin 1947). The Uro have been historically discriminated against (La Barre 1947; Osborne 1952) due to their aquatic lifestyle (Forbes 1870; La

Barre 1947). There is also a small white and mixed race, or mestizo, population, which historically occupied most positions of influence (Tschopik 1947).

The ethnobiological literature shows that there can be differences in LEK between speakers of different languages (Inglis and Pascual 2021). What languages people speak, and which they primarily speak at home, is often associated with acculturation with Western or local culture (Kik et al. 2021). Historically, most residents in the Altiplano would have spoken Quechua or Aymara, but the spread of education and mass media means more people speak Spanish.

Statistical Methods

We constructed generalised linear mixed models (GLMM) with the above-mentioned fixed effects. We included the location of the interview as a random effect to control for the non-independence of samples taken within the same village. Although results from Likert Scales are ordinal, the number of categories included is high enough that they can be treated as continuous (Sullivan and Artino 2013). We tested for collinearity of explanatory variables using variance inflation factor (VIF) of all categories and found them to have a VIF of under 5, meaning they could be included without risking multicollinearity (Akinwande, Dikko and Samson 2015).

Dependent variables in these analyses were (a) the peoples' opinion of the Titicaca Grebe on the Likert Scale, (b) self-assessed knowledge of the Titicaca Grebe on the Likert Scale, (c) Knowledge of whether the Titicaca Grebe is endangered as a binary yes/no answer, (d) knowledge as to whether the Titicaca Grebe is endemic or not as a binary yes/no answer, and (e) willingness to conserve the grebe before being told that it was endangered or endemic as a binary yes/no answer. The GLMMs of analyses 3–5 had a binomial distribution with a logit link function, and the GLMMs of analysis 1 and 2 had a Poisson distribution with a log link function. Complex missed effects models tend to fail to converge and produce singular fits. Where this occurred, we used backwards stepwise elimination to produce a maximum feasible model using the likelihood-ratio test (Matuschek et al. 2017).

We used an information theoretic approach in deciding which models to interpret in our results (Burnham et al. 2002). We submitted each global or maximum feasible model to an automated all subsets model selection, retaining random effects, and elected the best model based on the Akaike's information criterion corrected for small sample sizes (AICc).

We omitted respondents who said they did not know of the grebe either by name or when shown a picture ($N = 25$). We also performed a χ^2 test to determine if there was a difference in the number of individuals who claimed to favour conservation of the Titicaca Grebe before and after being told of its endemic and endangered status. To correct for multiple analyses, we applied Holm–Bonferroni corrections (Holm 1979) to the GLMMs. Statistical analysis was conducted in R, using the lmer, MuMIn, and buildmer packages (Bárton 2013; Bates et al. 2015; Voeten 2021).

Qualitative Methods

Interviewees were asked to justify their opinion of the grebe and to justify their self-assessed knowledge of the grebe. A total of 221 semi-structured interviews were conducted, using a guided survey questionnaire, but also allowing for open-ended responses. Respondents' identities were anonymised to promote open responses and their demographic information is detailed in the following section. We used an inductive, bottom-up approach to assess the qualitative results to better understand the context in which the interlocutors operate. We performed thematic analysis of interviewee responses to identify three key themes that emerged (Creswell and Creswell 2018). The three themes entailed attitudes and behaviours towards the grebe, economic indicators that differentiated knowledge about the grebe, and conservation education-based responses concerning the intrinsic value of the grebe. The thematic coding allowed us to tease out the reasons for people's opinions of the grebe (Newing 2011; Thomsen et al. 2021).

The authors include speakers of Aymara and Quechua. The degree to which various authors speak the language varies, from Author D. A. V., who learnt Quechua and Aymara as an adult, to Authors A. M. and M. A. V., who are first-language Aymara speakers and who grew up in the Altiplano region. Of the authors, only authors A. M. and M. A. V. primarily reside in the rural Altiplano region around Lake Titicaca, though Authors E. R. G. T. and E. G. M. T. live in Puno, author P. V. N. lives in La Paz. Interviews were conducted in the towns where Authors A. M. and M. A. V. reside, though they are originally from different towns in the Altiplano. The communities which were sampled were primarily rural villages, of a few hundred or at most a few thousand inhabitants. In most of them, the primary profession of most individuals is farming, though almost all of them have a nucleus of artisans and traders. They are primarily Aymara speaking rather than Quechua speaking, as reflects the demographics of the Altiplano region. Being on the lakeside, most of them have significant numbers of fishers in addition to agriculturalists, and many people partake of both activities. Almost all have weekly markets, where farmers from more remote homesteads come to sell their wares and purchase goods which cannot be made at home. Within living memory, most of these communities would have lacked electricity, running water, or paved roads connecting them to the outside world. However, all now have these amenities, and all of them also have fast cellular signal, which is regularly used by locals to conduct trade and communicate. The Altiplano region is undergoing rapid cultural and economic change, leading to significant changes in LEK (Villar et al. 2024), meaning that these surveys provide a snapshot of a society in transition from the staid routines of tradition to the more hectic patterns of a market-driven life. Socially, these communities tend to be highly distrustful of outsiders,

meaning anyone not from said village. The authors had to negotiate permissions to enter and conduct research in each village, and were on multiple occasions accused of being gold prospectors. In many villages, young people are scarce, as they have moved to mining regions or cities for economic opportunities. Because of this, there are tracts of fallow land around many villages. However, these generalisations should not distract from how each village is distinct and unique. For instance, Santiago de Okola has adapted to tourism more than most other villages on the Bolivian side of the border, Guaqui has a military base that employs many residents, and Isla Suriqui is a centre of boat building in the region.

Results

Demographic Results

In total, we interviewed 221 interlocutors across 23 sites over the course of 6 months, in interviews ranging in time from 15 min to 2 hours. Of these, 196 had heard of the Titicaca Grebe either by name or photo. Forty-eight respondents recognised the official Spanish name *Zambullidor del Titicaca*, and 148 recognised the grebe by photo. Ten respondents who were familiar with the grebe but did not know any specific name; this number does not include those who gave it a generic name, such as *pato*. Of the rest, the most given names were keñola or queñola (N = 43), keñokea (N = 23), pato or patito (N = 21), keñokaya (N = 13), and choka (N = 8). All terms were used by Quechua and Aymara speakers, suggesting a shared vocabulary for waterfowl in the region.

Statistical Results

The average rating of the grebe was 6.2 on the Likert Scale, and the average self-assessed knowledge was 4.9 on the Likert Scale. Full results can be seen in Figures 2 and 3.

The global model for opinion of the grebe failed to converge, and backwards stepwise elimination produced a maximum feasible model which included profession and religion, and the model with the lowest AIC_C only included profession category. AIC_c value tables for this, and all other GLMMs, are in the Supplemental Materials. Being involved in fisheries had a significant negative effect on opinion of the grebe (Table 1).

The global model for self-assessed knowledge failed to converge, and backwards stepwise elimination produced a maximum feasible model which included involvement in profession country, sex, and residence status, and the model with the lowest AIC_C included all these variables. Being male and being resident in the same town as where one was born significantly increased self-assessed knowledge of the grebe (Table 2).

One hundred forty-nine individuals wanted to conserve the grebe before being told that it was endangered or endemic. The GLMM failed to converge, and the maximal feasible model only included profession category, though none were significant (Table 3).

Ninety-seven individuals knew that the grebe was endangered. The GLMM failed to converge, and the maximal feasible model included education, religion, and country. The model with the lowest AIC_C included all these variables, though none were significant (Table 4).

Eighty-one individuals knew that the grebe was endemic. The GLMM failed to converge, and the maximal feasible model included country, family size, profession category, religion, and sex. The model with the lowest AIC_C included country, family size, and sex, of which being Peruvian was significantly associated with knowing the grebe was endemic (Table 5).

After having been told that the grebe was endangered and endemic, no individual who had previously supported grebe conservation said that they were opposed to conservation. Thirteen of the 47 who had been opposed to the grebe's conservation said they were now in favour of conserving it ($\chi^2 = 2.576$, df = 1, P = 0.108).

Qualitative Results

Many interlocutors did not care about the Titicaca Grebe. This was not because they disliked it, but because they had little interest in nature. The comments of Interviewee #71 in Tito Yupanqui, Bolivia, are typical – 'it does not affect my life, so I do not care about it'.[1]

Amongst those who liked the grebe, most viewed it as innocuous. The view of a woman in Isla Suriqui, Bolivia, was typical when she said that the grebe 'does not do any harm'.[2] We found three main positive traits associated with the grebe. The most common positive comment was that it was pretty, with some people saying that they enjoyed watching it as it dives. Another positive attribute of the bird was that since it was local and Andean, it must be protected by local and Andean peoples. This view was put by a 66-year-old Aymara man in Puerto Pérez, Bolivia, who said that the bird should be protected because it 'is Andean, and it is ancestral to us'.[3] Finally, some said the bird was part of a wider ecosystem, and thus had a role which meant it should be protected. This view was expressed by a 54-year-old Quechua man in Llachon, Peru, who said 'it is an indispensable part of the ecosystem'.[4] Three people, one in Guaqui, Bolivia, one in Carabuco, Bolivia, and one in Huatajata, Bolivia, mentioned tourism as an economic benefit of the grebe. Two people mentioned any practical uses of the grebe, one in Puerto Acosta, Bolivia and one in Taraco, Bolivia. In both cases, they said that the grebe's cry was a warning sign for bad weather on the lake.

Negative views of the grebe mainly came from fishers. Fishers viewed the grebe as competition for dwindling numbers of fish, and due to the damage they do to nets when caught as bycatch. This view of the grebe, as a nuisance animal, is summed up by a fisher in Huatajata, Bolivia, who said that the grebe 'breaks nets, eats fish, and can't be eaten'.[5] This hostility to the grebe was on display in the

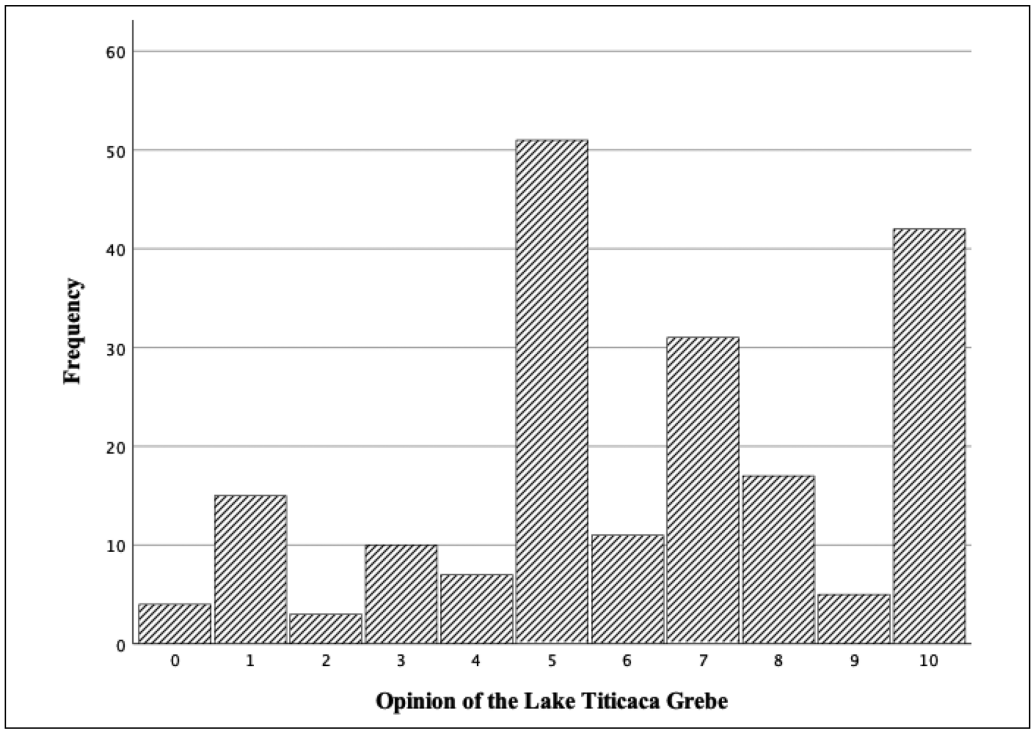


Figure 2. Distribution of Likert scale (0 = most dislike to 10 = greatest like) responses on opinion of the Titicaca Grebe.

monthly meeting of the heads of fishing villages in Puno, Peru, where the lead author heard a room full of heads of fishing associations state various reasons why conservation of the grebe would be a terrible idea. Non-fishers' hostility to the grebe tended to stem from problems which fisher relatives had with grebes falling in their nets and competing with them for fish, or from a general dislike of wildlife. All fishers who expressed extreme dislike of the grebe were Aymara and Quechua. Uros were willing to discuss the grebe, but were more reticent to engage in surveys, making the quantitative sample size of Uro responses low. Further research should inquire about the effects of intra-Indigenous group dynamics on grebe conservation, which is beyond the scope of this article.

Most people provided very limited natural history knowledge of the Titicaca Grebe, independent of self-assessed knowledge. Usually, this was that the grebe lived in water or in the aquatic vegetation, or that it ate fish. Others also commented on how long it could stay in the water for, with some claiming to have seen the grebe staying underwater for several minutes. Several observations of grebe behaviour, not in the ornithological literature, were provided. One included how the species provides parental care, such as carrying its young on its back and throwing them in the water and rushing off in the opposite direction to them as a form of distraction when attacked by Andean gulls seeking to prey upon chicks. This was attested to by multiple people and was witnessed by the authors. Locals also seemed to be aware of a breeding season for the grebe, with multiple people mentioning that eggs are laid between August and October. This is contra the ornithological literature which says the grebe breeds year-round (Fjeldså 1981, 2004; Martinez, Aranibar and Gutierrez 2006). Subsequent field observations of the grebe has verified that the grebe has a breeding season which is concurrent with the Altiplano's rainy season, which usually runs from August to October (D. A. V., pers. obvs.). Several older individuals mentioned that the grebe used to be much more common, while younger people indicated there were more now.

Discussion

While the literature often portrays human–wildlife conflict or co-existence in binary terms, here we show that both exist

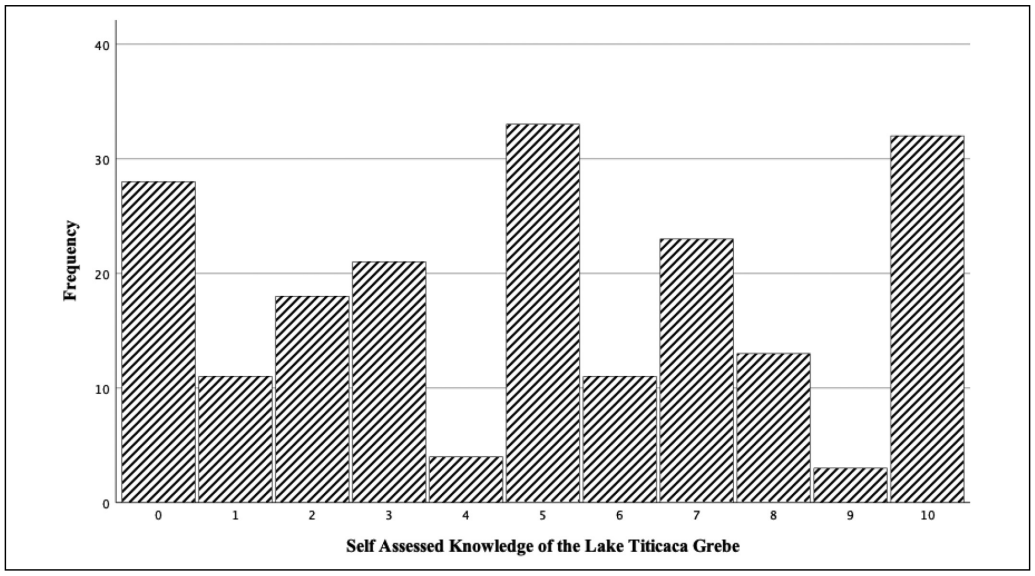


Figure 3. Distribution of Likert scale (0 = least knowledge to 10 = most knowledge) responses on self-assessed knowledge of the Titicaca Grebe.

Table 1. Results of the Optimised GLMM Looking at Factors Affecting Opinion of the Titicaca Grebe, on a Likert Scale (1–10).

Category	Estimate	Standard error	z value	P
(Intercept)	**1.9742**	**0.0730**	**27.06**	**~ 0.00 (2e−16)**
Animal husbandry	−0.1042	0.1123	−0.93	~ 1.00 (0.350)
Business	−0.1608	0.1065	−1.51	~ 1.00 (0.13)
Fisheries	**−0.4837**	**0.1015**	**−4.77**	**0.0001 (1.9e−06)**
Homemaker	−0.0245	0.1158	−0.21	~ 1.00 (0.83)
Miscellaneous	−0.0414	0.1358	−0.30	~ 1.00 (0.76)
Professional	0.1543	0.1228	1.26	~ 1.00 (0.21)
Skilled manual labour	−0.0315	0.1129	−0.28	~ 1.00 (0.78)
Tourism	−0.4387	0.2425	−1.81	~ 1.00 (0.07)
Unskilled manual labour	−0.1819	0.1791	−1.02	~ 1.00 (0.31)

AIC_c 972. Significant values in bold. Non-Holm–Bonferroni corrected *P* values in parentheses.

simultaneously within a society. Most people were apathetic about the grebe, having a passive coexistence with it. While apathy is not as severe a conservation issue as hostility, it can still be a problem (Holladay and Ormsby 2011; Kwan et al. 2017). Apathy reduces the willingness of people to change

Table 2. Results of the Optimised GLMM Looking at Factors Affecting Self-Assessed Knowledge of the Titicaca Grebe, on a Likert Scale (1–10).

Category	Estimate	Standard error	z value	P
(Intercept)	**0.6919**	**0.1552**	**4.46**	**0.0002 (3e−06)**
Animal husbandry	0.4378	0.1391	3.15	0.0736 (0.0016)
Business	−0.2757	0.1639	−1.68	~ 1.00 (0.926)
Fisheries	0.3410	0.1158	2.94	0.1440 (0.0032)
Homemaker	0.3484	0.1529	2.28	0.9307 (0.0227)
Miscellaneous	0.2648	0.1665	1.59	~ 1.00 (0.1119)
Professional	0.3682	0.1545	2.38	0.7396 (0.0172)
Skilled manual labour	−0.1500	0.1622	−0.92	~ 1.00 (0.3551)
Tourism	0.1977	0.2354	0.84	~ 1.00 (0.4011)
Unskilled manual labour	−0.0418	0.2384	−0.18	~ 1.00 (0.8608)
Peru	0.3197	0.1377	2.32	0.8526 (0.0203)
Residence same as birthplace	**0.3394**	**0.0848**	**4.00**	**0.0031 (6.3e−05)**
Male	**0.4745**	**0.0965**	**4.92**	**4.6e−5 (8.8e−07)**

AIC_c 1062. Significant values in bold. Non-Holm–Bonferroni corrected P values in parentheses.

Table 3. Results of the Optimised GLMM Looking at Factors Affecting Willingness to Conserve the Titicaca Grebe Before Being Told it was Endemic or Endangered.

Category	Estimate	Standard error	z value	P
(Intercept)	1.504	0.547	2.75	0.2596 (0.0059)
Animal husbandry	−0.709	0.743	−0.95	~ 1.00 (0.3401)
Business	0.596	0.758	0.79	~ 1.00 (0.4322)
Fisheries	−1.327	0.613	−2.17	~ 1.00 (0.0303)
Homemaker	1.429	1.155	1.24	~ 1.00 (0.2161)
Miscellaneous	1.069	1.207	0.89	~ 1.00 (0.3756)
Professional	17.927	418.047	0.04	~ 1.00 (0.9658)
Skilled manual labour	0.950	0.916	1.04	~ 1.00 (0.3000)
Tourism	−0.602	1.322	−0.46	~ 1.00 (0.6488)
Unskilled manual labour	−0.206	1.318	−0.16	~ 1.00 (0.8760)

AIC_c 207. Significant values in bold. Non-Holm–Bonferroni corrected P values in parentheses.

routines or assist in conservation efforts, making those efforts which do occur overly reliant on a few individuals (Holladay and Ormsby 2011). Apathy is generally seen to result from a lack of education (Kwan et al. 2017), though it can also be due to a western-style education which only finds value in profit. We found some evidence for the former. While many people rated themselves highly when asked their self-knowledge of the grebe, when asked about whether the grebe was either endangered or endemic, most (72.4%) admitted that they had not known at least one of these facts. This suggests that there is a role for environmental education in teaching that the grebe is endangered and endemic. However, there are limits to this type of environmental education – only 13 out of 47 people who opposed conservation of the grebe changed their mind after being told that it was endangered and endemic.

Fishers' dislike of the grebe, though not representative of the wider community's views, was seemingly motivated by material forces (Harris 1980). The grebe conflicted with fishers as competition for fish, and as a damager of their nets. There is an extensive literature on terrestrial problem species (Nyhus 2016), but there is less literature on aquatic problem species (Blaber et al. 2009; Gandini and Frere 2012; Guerra 2019). A parallel to fisher–wildlife conflict is farmer–wildlife conflict; literature from those conflicts suggests that while the amount of damage is significant in influencing dislike (Inskip and Zimmermann 2009; Nyhus 2016), it does not explain all of it. The perception of damage is enough to fuel opposition to conservation, independent of levels of damage (Thomsen 2022; Treves et al. 2017). This perception is itself driven by attitudes, such as the ones which we have studied in this paper. Species which people are already predisposed to dislike are blamed for damage even when they do not do it, while those which people like are not blamed for damage they might actually do.

Table 4. Results of the Optimised GLMM Looking at Factors Affecting Knowledge That the Grebe is Endangered.

Category	Estimate	Standard error	z value	P
(Intercept)	1.64e+01	3.99e+03	0.00	~ 1.00 (0.9967)
Incomplete primary	−9.90e-03	8.54e−01	−0.01	~ 1.00 (0.9908)
Complete primary	6.64e−01	8.24e−01	0.81	~ 1.00 (0.4203)
Incomplete secondary	−1.92e+01	9.87e+03	0.00	~ 1.00 (0.9985)
Complete secondary	3.61e−01	7.76e−01	0.47	~ 1.00 (0.6415)
Incomplete technical	1.40e+00	8.65e−01	1.62	~ 1.00 (0.1060)
Complete technical	9.56e−01	1.12e+00	0.86	~ 1.00 (0.3916)
Incomplete university	2.16e+00	1.48e+00	1.47	~ 1.00 (0.1425)
Complete university	1.94e+01	3.25e+03	0.01	~ 1.00 (0.9952)
Atheist	−1.99e+01	3.99e+03	0.00	~ 1.00 (0.9960)
Roman Catholic	−1.76e+01	3.99e+03	0.00	~ 1.00 (0.9965)
Unspecified Protestant	−5.84e+01	4.71e+04	0.00	~ 1.00 (0.9990)
Pentecostal	−1.71e+01	3.99e+03	0.00	~ 1.00 (0.9966)
Nature-Worship	2.17e+00	1.29e+04	0.00	~ 1.00 (0.9999)
Methodist	−3.43e+01	7.01e+03	0.00	~ 1.00 (0.9961)
Seventh Day Adventist	−3.27e−01	9.27e+03	0.00	~ 1.00 (0.9999)
Peru	1.47e+00	5.62e−01	2.62	~ 1.00 (0.9999)

AIC_c 259. Significant values in Bold. Non-Holm–Bonferroni corrected P values in parentheses.

Table 5. Results of the Optimised GLMM Looking at Factors Affecting Knowledge That the Grebe is Endemic.

Category	Estimate	Standard error	z value	P
(Intercept)	**−2.9503**	**0.6501**	**−4.54**	**0.0003 (5.7e−06)**
Peru	**2.3570**	**0.6304**	**3.74**	**0.0086 (0.0002)**
Male	1.4331	0.4426	3.24	0.0569 (0.00121)
Family size	0.1861	0.0877	2.12	~1.00 (0.03388)

AIC_c 227. Significant values in bold. Non-Holm–Bonferroni corrected P values in parentheses.

Those who liked the grebe often spoke of its aesthetic value, which while a common defence of conservation (Tribot, Deter and Mouquet 2018), is not easily converted to policies to change attitudes. Identification of the grebe with the Lake Titicaca region, including its people, may be more useful. Conservation has often been promoted by identifying a species with a people (Hammerschlag and Gallagher 2017), and perhaps by making the Titicaca Grebe a symbol of the Titicaca region, its conservation could be aided. This would lead to a positive cultural coexistence, as seen in other areas where wildlife that can harm people have a high degree of cultural saliency (Dhee et al. 2019).

The differences between younger and older respondents in how they viewed population trends of the grebe is evidence of shifting baseline syndrome (Pauly 1995). Shifting baseline syndrome is where people believe that their lived experiences are normal, causing the baseline for 'natural' ecosystems to shift over time. Older residents said the population of the Titicaca Grebe had declined, which is consistent with the decline in grebe populations between 1970 and 2000 (Engblom et al. 2001). Younger respondents said the grebe's population had increased. This suggests that there may have been a population recovery of the grebe since a low point in the early twenty-first century, but that this recovery is not to the level which the grebe had before the introduction of commercial fisheries. Shifting baselines can artificially influence degraded ecosystems as optimal conservation programme targets (Jones et al. 2020). In the case of the Titicaca Grebe, conservation targets should consider the pre-industrial population as the goal, rather than the recently recovered population.

Conclusion

Conservation is about people as much as it is about wildlife. However, the literature can at times treat many human groups, particularly indigenous ones, as monoliths in human–wildlife relations. Here, pluralistic attitudes leading to conflict and coexistence do exist within indigenous societies. Most local people expressed apathy towards the Titicaca Grebe, leading to passive coexistence, apathy defined as a score between 4 and 6. Conflict was driven by fishers' self-perceived economic interests and is likely to be a significant barrier to conservation of the species. Environmental education that focuses on the Grebe's Andean status could help conservation efforts by fostering a more positive, active coexistence. Further research is needed to determine if intra-fisher dislike is driven by objective bycatch numbers, and on how to mitigate both bycatch and perceived competition between fishers and grebes.

This article provides insights into how future studies can approach Indigenous–wildlife conflict and coexistence not as a dichotomy that exists between cultures, but as a spectrum of opinion that exists within them – like any other human culture. Indigenous cultures and languages should be respected and given equal standing in human–wildlife relations (Thomsen et al. 2023), but we must also recognise individual agency and how this affects intra-cultural diversity of opinion and knowledge of wildlife. Only then can we better understand how cultural drivers engender human–wildlife coexistence not just in the Altiplano, but in context-specific cases globally.

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Supplemental Material

Supplemental material for this article is available online.

Notes

1. No me afecta mi vida, no me importa
2. No hace daño
3. Es ave andino y ancestral
4. Es indispensable para el ecosistema
5. Come peces, rompe las redes, y no se puede comer

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The data used in this paper can be found in appendix B

5

Declining Use of Totora (*Schoenoplectus californicus* subsp *tatora*) in Lake Titicaca

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Declining Use of Totora (*Schoenoplectus californicus* subsp *tatora*) in Lake Titicaca

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Abstract
Local Ecological Knowledge (LEK) is fast disappearing globally but the drivers of this loss are not fully understood. We present a a case study of how even long-standing and regulated forms of LEK are vulnerable to erosion as market forces spread to regions which have historically been peripheral to global markets.We consider changes in knowledge and use of a cultural keystone species, totora, in the Altiplano of Bolivia and Peru around Lake Titicaca. Totora has been used for a variety of purposes and historically its cultivation and planting was regulated by village co-operative councils, called *ayllus*. We argue that a significant decline in the use of totora in the Altiplano along with the disappearance of the regulatory power of *ayllus* have primarily been driven by the integration of the Altiplano into the global market system, which has led to the replacement of totora with industrially manufactured goods, such as plastics and concrete. It has also undermined social bonds as individuals rather than the ayllu become the fundamental agents of economic decision-making.

Keywords Traditional ecological knowledge · *Ayllu* · Loss of traditional knowledge · Totora · Altiplano · Lake Titicaca · Peru · Bolivia

Introduction

Traditional Ecological Knowledge (TEK) and Local Ecological Knowledge (LEK) both comprise knowledge of the natural world discerned through direct interaction over extended periods of time (Berkes et al., 2000; Brook & McLachlan, 2008). Definitions vary substantially, and whether they can be meaningfully distinguished is the subject of ongoing academic debate (Souto & Ticktin, 2012). However, there is widespread recognition of their increasing erosion worldwide (Leony & Voeks, 2004; Aparicio Aparicio et al., 2021). The drivers of this loss are various, but include formal education (Voeks & Leony, 2004; Aparicio Aparicio et al., 2021), urbanisation (Sogbohossou et al., 2015; Gosler & Tilling, 2022), changing gender roles (Souto & Ticktin, 2012; Brandt et al., 2013; Aparicio Aparicio et al., 2021), socio-economic changes (Aparicio Aparicio et al., 2021), age (Voeks & Leony, 2004; Souto & Ticktin, 2012; Brandt et al., 2013; Aparicio Aparicio et al., 2021), ethnic interactions (Eyssartier et al., 2008), changes in religious practice (Rist et al., 2003; Gruberg et al., 2022), and migration patterns (Souto & Ticktin, 2012; Brandt et al., 2013; Aparicio Aparicio et al., 2021). The most studied drivers

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of loss of TEK have been the effects of age and education. While most studies have found that the young have less ethnobotanical knowledge than the old, there is disagreement about how to interpret these findings. Some argue that it indicates a loss of ethnobotanical knowledge (Begossi et al., 2002; Aparicio Aparicio, 2021), while others argue that ethnobotanical knowledge may be gained over a lifetime, making low scores of ethnobotanical knowledge among the young misleading (Voeks & Leony, 2004; Quinlan & Quinlan, 2007). There is less debate, however, over the decline in the habitual use of traditional botanical sources – even among those who know the properties and traditional uses of plants (Voeks & Leony, 2004; Aparicio Aparicio, 2021).

Most ethnobotanical studies have focused on a suite of plants that are used or known about by individuals in one geographic area or ethnic group (Begossi et al., 2002; Mathez-Stiefel et al., 2012; Aparicio Aparicio et al., 2021; Gruberg et al., 2022). Here, we focus on the use of one plant: the Totora reed (*Schoenoplectus spp.*). Single species studies have some disadvantages over multi-species studies, such as not incorporating all types of TEK that exist within a community, relationships among species, and the inability to compare changes of use between types of use or species. But they can allow researchers to understand in greater detail the drivers of changes of use (Banack et al., 2004; Brandt et al., 2013; Sogbohossou et al., 2015). This is especially useful when studying species that are, or until recently were, culturally or economically important keystone species, i.e., species particularly important for ecosystem function (Paine, 1966), or, in the case of cultural keystone species, particularly central to the functioning of a particular human culture or group (Garibaldi & Turner, 2004). Focusing on well-documented species can also allow for direct historical comparison of uses.

Totora, generally identified as *Schoenoplectus californicus*, subp. *tatora* (Banack et al., 2004), but likely to be multiple species of *Schoenoplectus* (P. V. N., pers. obs.), (Fig. 1) is a perennial aquatic sedge native to South America but is also now found as far north as California. It is an invasive plant in other parts of the world, such as New



Fig. 1 Totora in Lake Titicaca

Zealand (Heiser, 1974; de Lange et al., 1998). Totora has been a cultural keystone species for both the coastal and the lakeside communities of Peru, Bolivia, and Chile for several thousand years (Bruno et al., 2021; Stanish, 2003; Banack et al., 2004; Erickson, 2000; Macía & Balslev, 2000; Levieil & Orlove, 1990, 1992; Heiser, 1974, 1978; Forman, 1977; La Barre, 1941, 1948; Mishkin, 1946; Tschopik, 1946; Tutin, 1940; Forbes, 1870). Historically, totora has been used to create vessels (Stanish, 2003; La Barre, 1948; Mishkin, 1946), for roofing (Forbes, 1870; Gilson, 1938), as animal feed (Banack et al., 2004), and to produce artisanal goods, such as mats and baskets (Mishkin, 1946; La Barre, 1948; Banack et al., 2004). Totora is especially important culturally in the Altiplano region around Lake Titicaca. Though totora is not a domesticated plant, it was and is managed by the people of Lake Titicaca. This includes deliberate plantings where totora is absent, and burnings (Fig. 2) to encourage the growth of new totora stands during August and September (La Barre, 1948; Heiser, 1978; Erickson, 2000; Stanish, 2003; Banack et al., 2004). This long-term use, harvesting, and planting of totora by the indigenous people of the Altiplano gives us confidence that the communities' knowledge of totora meets the criteria of TEK (Berkes et al., 2000). We explore the drivers of changing uses of totora in the Lake Titicaca region, and consider how the decline of a once prominent cultural keystone species may reflect on other forms of Traditional and Local Ecological Knowledge in the Altiplano region of Peru and Bolivia.

Historical Ecology of the Totora and Altiplano Societies near Lake Titicaca

Ecological Importance of Totora

In addition to its cultural value, totora is an important ecosystem engineer in Lake Titicaca. Totora wetland is one of the major characteristic aquatic vegetative zones of the Lake (Tutin, 1940), dominating most of the area and a breeding habitat of the endemic Titicaca Grebe (*Rollandia*



Fig. 2 Smoke from totora burning in Peru in August, 2022

microptera) and the Titicaca Giant Frog (*Telmatobius culeus*), both of which are listed as endangered by the International Union for the Conservation of Nature (IUCN) (Villar et al., 2023; Fjeldså, 1981; Vellard, 1992). Totora wetlands are also thought to be an important habitat for many of fish, including endemic pupfish of the genus Orestias (Vila et al., 2007; Lauzanne, 1992). This ecosystem also provides shelter to many endemic invertebrates, most of which probably remain to be discovered (Jaume et al., 2021; Kroll et al., 2012; Boury-Esnault & Volkmer-Ribiero, 1992; Mourguiart, 1992; Dejoux, 1992). In addition to hosting these endemics, the totora wetlands of Lake Titicaca are an important habitat for many species of waterfowl, including the Andean Ruddyduck (*Oxyura ferruginea*), the Puna Teal (*Spatula Puna*), Slate-coloured Coot (*Fulica ardesiaca*), and White-tufted Grebe (*Rollandia rolland*), amongst others (Pulido Capurro, 2018; Fjeldså & Krabbe, 1990; Fjeldså, 1981). Despite the high cultural and biological importance of totora wetlands, it remains, like many high-altitude wetlands, critically understudied from a biological, ethnobiological, and conservation perspective (Aber et al., 2012; Harden & Fernández, 2022).

Situating Altiplano Societies

Lake Titicaca is the highest altitude navigable lake on earth and is the centre of the broader Altiplano cultural region, a broadly flat area of the central Andes between 3800 and 4000 m.a.s.l., a landscape that has been heavily modified by agricultural societies since at least 3,500 BP (Fig. 3) (Ellenberg, 1979; Kent et al., 1999). Totora appears to have been introduced by humans to Lake Titicaca from the Pacific coast around 3,500 BP (Erickson, 2000; Paduano et al., 2003; Bruno et al., 2021) and the paleopalynological record suggests that it has remained important for the human cultures of the lake. Early anthropological work showed that totora was most extensively used by the Uro ethnic group (Forbes, 1870; La Barre, 1948). Until recently, the Uro resided on floating islands of dried totora (La Barre, 1948; Orlove, 1991; Stanish, 2003; Banack et al., 2004), and many still own such islands, though now they are mainly operated for tourism. The Uro have historically been the poorest group around Lake Titicaca, and discrimination against them, even by other Indigenous people such as the Aymara and the Quechua, continues to be documented up to the

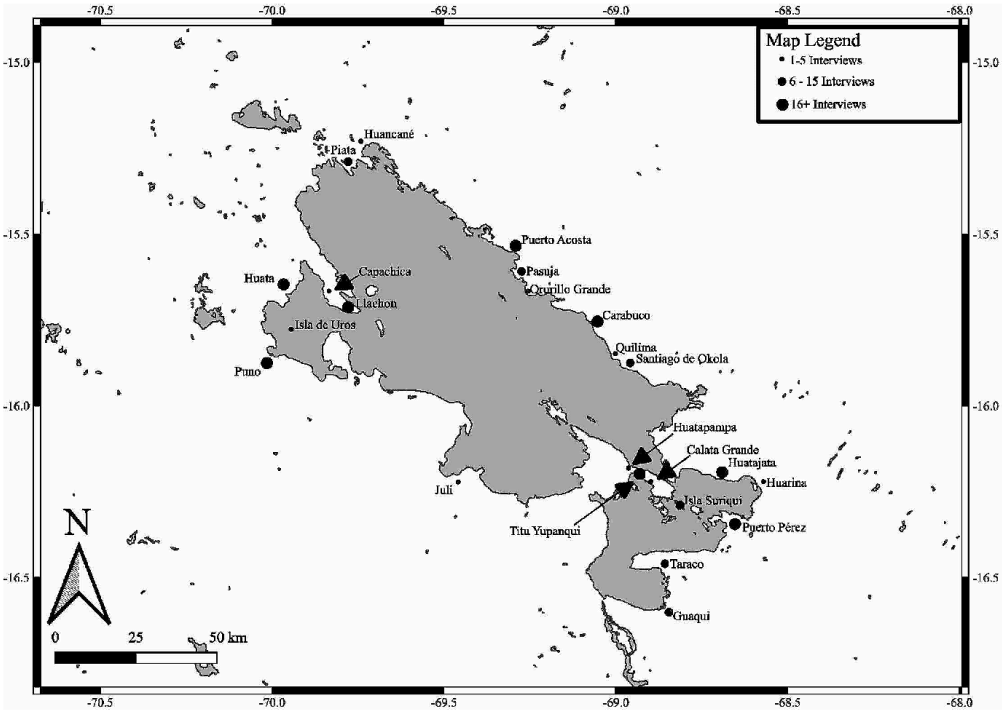


Fig. 3 Map of Lake Titicaca, with locations of interviews highlighted

present day (Kent, 2013; de Loma et al., 2019). This anti-Uro sentiment has been directly tied to the Uro's aquatic and semi-nomadic traditional lifestyle, which entails neither land ownership nor cultivation in the popular manner of the peoples of the Altiplano (La Barre, 1941; de la Saavedra et al., 2011; Lara Barrientos, 2012). This nomadic and semi-aquatic lifestyle is so predicated on the use and cultivation of totora, that the Peruvian government has given special rights to Uro communities to cultivate totoras in what are otherwise protected areas, including the Reserva Nacional del Titicaca (Orlove, 1991). The Uro have historically been the ethnic group around Lake Titicaca most reliant on totora, but two other dominant ethnic groups of the region, the Aymara, and the Quechua, have also historically used totora to make reed boats, as livestock feed, and for artisanal products (Forbes, 1870; Mishkin, 1946; Tschopik, 1946).

Historically, the management of totora has been communal, and organised through a clan-based governance system called *ayllu* (La Barre, 1948; Erickson, 2000; Banack et al., 2004), which has been, for most of the period since the Spanish conquest, the basic form of organisation of Altiplano society (Mishkin, 1946; Erickson, 2000). Its kinship structure centres on the extended families in each village and oversees communal properties such as grazing lands, fishing territories, and totora fields (Tschopik, 1946; Levieil & Orlove, 1990; Villarroel et al., 2014). Multiple attempts were made to outlaw *ayllus* in both Peru and Bolivia during the nineteenth and twentieth centuries (Tschopik, 1946; La Barre, 1948), and multiple failed predictions were made of its imminent collapse as a viable form of collective resource management (Mishkin, 1946; La Barre, 1948; Rist et al., 2003). Since the Bolivian Revolution of 1952 and the Peruvian Land Reform of 1969, both countries have officially recognised the legal rights of *ayllus* (Rist et al., 2003), and since 2009 these have been enshrined in the Bolivian constitution (Schilling-Vacaflor, 2011). The modern *ayllu* is thus more of an administrative unit that shares a name with this ancient collective mode of production (Eisenberg, 2013) than a direct transposition to the present day, and until recently was the primary means of regulating the use of totora in the Altiplano (Orlove, 2002; Banack et a., 2004).

Twenty years ago, Banack et al. (2004) found that totora was beginning to be harvested at greater intensity around Lake Titicaca than previously, and at levels that they considered unsustainable. They also documented several sustainable traditional practices of totora harvest, including annual burnings to remove older plants, and communal control of totora by *ayllus*, though they also noted an apparent weakening in the power of *ayllus* to regulate individual totora cultivation. They attributed the increasing intensity of totora harvest to the increasing population around Lake Titicaca. Since then, a generation has passed that has seen a further weakening of traditional economic structures but capitalistic gain that has been associated with reduced poverty and increased migration to urban areas in the Altiplano. The region has also seen significant political change, especially in Bolivia, where a socialist government has restructured society and the economy since 2006. Our objective was to determine what has changed in the cultivation and uses of totora, and whether the increased intensity of traditional harvesting techniques and uses described by Banack et al. have persisted during this period of rapid poverty reduction in the region as well as urbanisation, the growth of the tourism sector, the expansion of education, greater freedoms for women, decline in the birth-rate, and growth in Christian evangelicalism. While these differences have occurred on both the Peruvian and the Bolivian sides of Lake Titicaca (Webber, 2016),, there has been greater disruption of traditional patterns of living on the Bolivian side due to faster economic development in rural Bolivia since 2006.

Following previous work on demographic factors influencing loss of TEK in rapidly changing societies (Rist et al., 2003; Voeks & Leony, 2004; Brandt et al., 2013; Sogbohossou et al., 2015; Aparicio Aparicio et al., 2021; Gruberg et al., 2022) we hypothesised that country, sex, profession, religion, age, ethnicity, education, migrant status, language use, and family size could all potentially influence the degree of change in whether and how individuals use totora in the region. We first describe our materials and mixed methods before presenting our findings. We then discuss the potential effects that the declining use of totora as a cultural keystone species may have on contemporary Indigenous culture and knowledge.

Materials & Methods

Study Area

Lake Titicaca, the highest-altitude navigable lake on earth with a surface altitude of 3,812 m (Wirrmann, 1992), forms the core of the watershed that is the main source of water in the Altiplano. Lake Titicaca is shared between Peru and Bolivia. The lake is further divided into two major sub-lakes: Lago Mayor is the larger and includes all the deep-water sections of the lake, as well as the majority of the totora wetland (Wirrmann, 1992; Villar et al., 2023); and Lago Menor, a shallow lake with an average depth of nine metres (Wirrmann, 1992) and a higher degree of primary productivity for its area than Lago Mayor (Richerson et al., 1992). Lago Menor is also the region of Lake Titicaca with the longest archaeological record of totora use and fishing by humans (Bruno et al., 2021). The entirety of Lake Titicaca has seen increases in pollution in the last several decades (Guédron

et al., 2017, 2020), which might also influence the growth of totora, although the plant has proven resilient to pollution in other contexts (Blanco, 2019).

The Altiplano cultural landscape surrounds Lake Titicaca (Ellenberg, 1979; Young, 1997; Brown & Mitchell, 2000). Whether the the region may have been forested before agriculture remains debated, (Fjeldså, 2002; Kessler, 2002; Paduano et al., 2003; Gosling et al., 2009; Hanselman et al., 2011), but the naturally occurring vegetation now is Puna grassland (Pulgar Vidal, 1987; Ibarguchi, 2014), such as *Jarava ichu*, *Azorella compacta*, and *Festuca dolichophylla*. There are marked wet and dry seasons, with a dry austral winter and a wet austral summer (Pulgar Vidal, 1987). In addition to the grassland, the Altiplano is also home to many small lakes that may be important repositories for biodiversity, but remain understudied. There are also pockets of non-Puna ecosystems around the Altiplano, such as *bofedales* peatlands (Squeo et al., 2006) and isolated pockets of *Polylepis* (Fjeldså, 2002).

While Puna grassland is the current naturally occurring landscape around Lake Titicaca, most of the area remains used for agriculture, primarily by subsistence farmers, though sheep herding is also common (Morales Garzón, 2016; Rojas et al., 2014; Fagandini & Bazili, 2016). Most of the land has been used for agriculture since before the Spanish conquest (Erickson, 2000; Stanish, 2003), when Andes the mountain range was named for its agricultural terraces (Ellenberg, 1979). However, these terraces are now abandoned and many villages have become depopulated as young people move to the cities (D. A. V., pers. obvs.). This may be causing a renewed expansion of Puna grassland, as has occurred in other regions (Poyatos et al., 2003; Navarro & Pereira, 2012), including other parts of the Andes (Haller & Bender, 2015). To our knowledge, no such study has been done to test whether this is the case in the Altiplano.

Data Collection

We adopted a mixed methods approach to ethnographic data collection that included semi-structured interviews, participant observation, and archival research coupled with quantitative surveys (Creswell and Creswell, 2017). We conducted semi-structured interviews with individuals in Spanish or, in cases where individuals were monolingual in Aymara, with the aid of an interpreter. We interviewed a total of 221 individuals from 23 locations: 143 in Bolivia and 78 in Peru, over the course of six months. Interviews lasted between 15 min and two hours, and were conducted face-to-face, in Bolivia from March to June and in Peru from June to September in 2022. Responses were digitally recorded and transcribed after fieldwork by the first author. The interviewees were a convenience sample of the Altiplano population that we considered necessary due to the dispersed and rural nature of Altiplano population. Time constraints also prevented the creation of a mechanism to randomly sample the wider population. While this is not ideal, convenience sampling has been used previously in ethnobiological studies (e.g., Cruz et al., 2014, Gutiérrez Alonso et al., 2020), and is considered a valid way of collecting information on community ethnobiological knowledge (Creswell & Creswell, 2018). We collected demographic information (age, sex, birthplace, present community, ethnic group, education, main language & languages spoken, family size, profession, and family size) (Appendix 1). We then asked about current or prior personal use of totora and the regulation and cultivation of totora. During the dry season (August) we engaged in participant observation during totora collection. Ethical approval was obtained from the Departmento de Biología, Universidad Nacional del Altiplano en Puno (UNAP).

Quantitative Data Analysis

We constructed a Generalised Linear Mixed Model, with binomial distribution using a logit link function, with the fixed effects of country, gender, age, religion, ethnicity, residence, education, profession category, primary language, and household size, and the random effect of the birthplace, current place of residence, and location of the interview, and the dependent variable being either current or past use of totora. Since questions about totora collection management elicited a qualitative response, we did not subject it to statistical analysis (see supplemental materials 1). We tested for collinearity of these variables by measuring the variance inflation factor (VIF) of all categories and found all of them to have a VIF of under 5, which means that they could be included without risking multicollinearity (Akinwande et al., 2015). Since this study grew out of a wider study focused on the interaction between fishers and non-fishers with the aquatic resources of Lake Titicaca, profession is divided between those involved in fisheries and those who are not. Statistical analysis was conducted in SPSS Statistics and in R using the lme4 package (Bates et al., 2015).

Qualitative Data Analysis

We performed a thematic analysis of the qualitative data (Newing, 2011) of the correspondents' responses to assess how totora is used, and, in cases where individuals no longer used totora, why they stopped using it. Qualitative analysis involves a close reading of responses and allows us to tease out the causes of declining totora use as understood by our informants. DAV recorded daily field notes of participant observation and subsequently analysed them (Creswell

Table 1 Predictors of current use of totora by individuals (AIC = 314.5252)

Fixed Effect	F	df	Sig.
Country	0.260	1	0.611
Sex	0.011	1	0.989
Age	0.797	1	0.373
Religion	0.121	2	0.997
Ethnicity	0.069	3	0.976
Residence	0.302	1	0.584
Education	0.403	8	0.918
Profession	**4.538**	**1**	**0.034**
Primary Language	0.579	5	0.716
Family Size	0.405	10	0.943

Table 2 Predictors of an individual having ceased to use totora (AIC = 252.5479)

Fixed Effect	F	df	Sig.
Country	**4.000**	**1**	**0.049**
Sex	0.103	1	0.749
Age	0.018	1	0.893
Religion	0.269	8	0.949
Ethnicity	1.795	3	0.174
Residence	0.056	1	0.814
Education	0.736	8	0.807
Profession	**6.929**	**1**	**0.010**
Primary Language	1.488	5	0.215
Family Size	1.097	10	0.376

& Creswell, 2018) to compare present use of totora to the results of previous studies, including harvesting methods during the end of the dry season in August and September (Banack et al., 2004; Levieil & Orlove, 1992; Heiser, 1978; La Barre, 1948; Mishkin, 1946; Tschopik, 1946; La Barre, 1941; Tutin, 1940; Forbes, 1870). DAV translated responses into English, which were verified by the co-authors.

Results

Quantitative Results

One hundred and twelve of the 221 respondents said that they currently used totora, 45 said they had previously used totora but have now ceased, and 64 said that they had never used totora. None of our respondents mentioned the collective management of totora as described by past researchers (Levieil & Orlove, 1990; Banack et al., 2004). However, several did mention that they were aware of this totora management technique, or that it had been used in their village in the past. When asked how totora is managed, all respondents, said that there were individual plots owned by households or individuals and that people had absolute freedom to do as they wished with those plots. However, there does appear to be some degree of coordination of totora use between neighbouring plots, especially regarding planting totora in areas where there previously was none, and the annual burning of old totora in August and September., The most common response ($N = 98$) to a question about current use of totora was for feeding livestock, followed by traditional handicrafts ($N = 27$), and human consumption, especially of its white root, which was likened to cheese ($N = 14$). Several interviewees described multiple uses. Production of traditional handicrafts seems to be restricted primarily to areas where tourism has overtaken agriculture as the primary industry, such as the floating village of the Uro in Puno Bay, Llachon, in Peru, and Santiago de Okola, Huatajata, Guaqui, and Copacabana in Bolivia.

Of the variables studied, only profession had a statistically significant effect on whether individuals still cultivated totora. Those who did not engage in fishing were more likely to harvest totora than were other groups. Of these, the majority were agriculturalists, who harvest totora as feed for livestock (Table 1).

Profession and country had a significant effect on whether individuals had abandoned the use of totora. Bolivians were more likely than Peruvians to have ceased to use totora, and fishers were more likely to have abandoned the use of totora than other professions (Table 2).

Qualitative Findings

Most people in the Altiplano either currently use or previously used totora. However the number of people who still use totora and the uses to which it is put appear to have declined since the last published study on totora use in the Lake Titicaca region (Banack et al., 2004). Some respondents indicated that they were nostalgic for some uses of totora. One farmer in El Muelle, Bolivia, said that he missed "the taste of totora root, which young people today don't know"[1]. Some even indicated that they thought that some of the old totora products were of higher quality than modern products, such as one man in Huatajata, Bolivia, who said that "totora cushions are more comfortable than the ones you get now"[2]. Despite nostalgia from some elements of Altiplano society, there appears to be very little effort to restore the use of totora to its former prominence. The reason for this is perhaps clear enough; a colleague of the authors, who did not participate in the questionnaire but is a fisherman in the community of Chimu, Peru, and a park ranger at the Reserva Nacional del Titicaca, said "It's a lot

[1] El sabor del queso de totora, que ya los jóvenes no comen.

[2] Los colchones viejos de totora eran más cómodos que los que compras ahora.

of effort to make things from totora, easier to go to Puno and buy them"[3].

We found no evidence for the previously well documented collective management of totora through *ayllus*. Instead, totora management is now highly individualised with respondents saying that "each person controls their own totora"[4] or that "each person has their own parcel of totora, and they control it"[5]. Nonetheless, the *ayllu* has not completely disappeared but rather modernised as in at least some towns it appears to have been replaced by a town council, with *concejales* and *alcaldes* taking the place of *mallkus*. Interviewees were still aware of the old collective management of totora, but, as one in Calata Grande, Bolivia, commented the traditional collective management of totora was something that "used to exist, back when there was an *ayllu*"[6]. Almost every interviewee who used totora said that they used it for their own livestock, primarily sheep, cattle, and guinea pigs, though many of the older respondents said that they knew how to make things out of totora. A few respondents, primarily older fishermen, indicated that they still remembered how to make the famed totora boats that used to grace Lake Titicaca. However, even those who said that they knew how to make them indicated that the modern wooden boats, though more expensive, had significant advantages over the traditional totora boats akin to other forms of passive acculturation through technological advance (Thomsen et al., 2020), namely, that a totora boat would rot away and must be replaced every 1–2 years, and that a modern wooden boat could carry more people and fish.

Even among people who still use totora, we observed a change in the relationship with totora. Two brothers interviewed in the village of Huata, Peru, offer an example of how even traditional agricultural uses of totora have changed over time. Their primary profession revolves around cutting totora in Huata and selling it as animal feed to other villages, one of which, Llachon, has developed a communal tourism industry. Another informant in Llachon was an artisanal crafts maker, who sold totora products to tourists, commented "I don't know how totora is harvested, I buy it"[7]. Artisanal uses of totora have also changed. During the entire study, we saw no practical artisanal objects made of totora apart from some totora covered couches in the hallways of some town halls, but rather, in regions with plenty of tourists, objects made with tourists in mind, such as miniature totora boats even although, ironically, there are no actual boats made of totora. There were, however, modern wooden boats with totora placed atop for decoration – which immediately marked them apart from the more common workaday fishing vessels of the region.

[3] Es mucho esfuerzo hacer cosas de totora, más fácil ir de compras en Puno.

[4] Cada uno controla su propria totora.

[5] Cada persona tiene su parcela de totora que lo contrala.

[6] Antes había cuando existía el ayllu.

[7] No se como se saca o se regula, lo compro.

Discussion

Economic Implications of Totora Use

In the Altiplano, whether an individual uses totora is primarily determined by their economic situation, with agriculturists being the last population in the region who have a practical reason to harvest totora as livestock feed in the winter. The other traditional uses of totora, such as roofing or practical items, seem to have been abandoned by the people of Lake Titicaca. Like other losses in traditional practices worldwide, this seems to have been driven by globalisation and materialised locally through rapid urbanisation and (eco)tourism (Vandebroek & Balick, 2012). In the Altiplano, it is now easier and cheaper to obtain industrially produced goods, such as corrugated aluminium roofs and plastics, than it is to produce these goods domestically using totora. This is not the first time that rapid cultural changes with ecological implications driven by economic changes have been noted in the Andes (Zimmerer, 1991, 1993). In each case, globalisation changed the incentive structures that permitted traditional resource uses to maintain themselves, either in the form of cheaper imported goods, or a greater outflow of labour to industry elsewhere.

Altiplano agriculture remains small-scale, but as the region develops, we expect that it will follow the trajectory of other countries and become industrialised, leading to the concentration into fewer, larger farms (Lianos, 1984; Beckett, 1990; Hobsbawm, 1994; Singh, 1997; Bryer, 2006). Once this occurs, the last remaining practical use of totora will be lost, and the use of totora in Lake Titicaca for practical purposes on a large scale will likely cease. In its place will be a niche market for totora, likely centred around tourism. To a degree, this has already happened for some uses, such as totora handicrafts and faux totora vessels.

It should be noted that the scale of loss of use of totora we have documented is likely an underestimate, since we interviewed only people in the Lake Titicaca area, and none who have migrated from area to cities, mining districts, the Amazonian agricultural frontier, or abroad. These migrants represent a significant percentage of the region's young people, especially young men, and in some villages constitute a majority of those who grew up there in the last decade and can safely be assumed to have abandoned any use of a plant that does not grow near their new locations.

It is perhaps ironic that there were more interviewees self-reporting that they have ceased using totora in Bolivia than in Peru because since 2006 Bolivia has, with one slight interruption, been governed by the Moviemento al Socialismo (MAS) a self-described socialist and Indigenous party. The Altiplano study region has been one of the significant political bastions of MAS, which since coming to power, strengthened the legal rights of indigenous institutions (Humphreys, 2017), and enshrined elements of Andean cosmovision, such as La Pachamama and Sumak Kawsay, into the Bolivian constitution (Barié, 2014; Humphreys, 2017). Admittedly, the MAS government has not always been honoured this commitment to Indigenous rights (Hope, 2016; Lalander, 2017; Hope, 2021), and despite their rhetorical commitment to the Indigenista ideology, it appears that loss of TEK is more rapid in Bolivia than in Peru, at least concerning totora among our interviewees. This suggests that economic development and prosperity, independent of ideology, is a significant driver of the loss of TEK.

Fishing as Mechanism toward a Market Economy in Lake Titicaca

There is evidence of fishing in Lake Titicaca in the archaeological record since the arrival of humans in the area (Capriles et al., 2008, 2014). However, it was traditionally a relatively unimportant economic activity (Young, 1997; Moore, 2011; Miller et al., 2021). This changed in the twentieth century with the introduction of pejerrey (*Odonesthes bonairensis*) and trout (*Salmo trutta*), which caused a fishing boom (Everett, 1973; Laba, 1979) that led not only to many individuals who had not previously fished becoming fishers, but also to modernisation of the lake's fishing fleet (Orlove, 2002). While the original fishing boom collapsed in the 1980s, last decade has seen a second fishing boom, this time with farmed fish. While both fishing booms have been capital-intensive, the second appears to require more start-up capital for people to get involved. We therefore suggest that the higher rate of abandonment of the use of totora by self-described fishermen may be due to them having sold off livestock to raise the capital needed to invest in fishing and fish farming.

One of our more intriguing findings is the apparent collapse of the *ayllu* as an organising economic principle over the course of a generation. In not a single village did we find collective management of totora – our respondents reported at most agreements between neighbours about the timing of burning, but even that is a significantly lower degree of cooperative management than described in previous studies (Forbes, 1870; La Barre, 1948; Levieil & Orlove, 1990; Banack et al., 2004). That is not to say that the *ayllu* has disappeared across the entire Altiplano – it still serves a local judicial function, though that also seems to be declining, and many people still identify with their *ayllu*. Furthermore, certain elements of communal lands appear to remain under the jurisdiction of *ayllus*, such as grazing territories (Eisenberg, 2013). Despite the *ayllus* having greater legal rights now than at any other time in the post-Spanish history of Peru or Bolivia, their economic power seems to be collapsing as the Altiplano increasingly integrates into the global market economy. It appears that capitalism ultimately cannot be resisted by collectively managed modes of production and that the *ayllu*, which has been praised by communists and anarchists alike as one of the few remaining examples of collective ownership and management of economic resources (Castro Pozo, 1924; Mariátegui, 1971 [1928]; Boudin, 1961; Carrière, 2010; Fabricant, 2010), could only survive as long as the rural Altiplano remained so peripheral to capitalism as to effectively be excluded from it. As has occurred elsewhere, increased integration with global markets has weakened the traditional natural resource regulatory functions of the *ayllu* (Moore, 1970; Brantlinger, 2018; Thomsen et al., 2021) despite theoretically left-of-centre governments in both Bolivia and Peru.

The aforementioned professional totora cutters are illustrative of the specialisation of totora use, even amongst those who are still using totora in relatively traditional ways. The brothers have specialised, and their customers no longer know much about totora, the plant, or how its harvested. Previous anthropological work on the economy of the Altiplano suggested that the cutting and cultivation of totora was a communal activity (Banack et al., 2004; Orlove, 2002; la Barre, 1948; Forbes, 1870). However, our interviews with the two brothers in Huata, Peru, who now specialise in totora cutting and with the artisanal crafts maker who buys totora to create products to sell to tourists indicate a rise of specialisation and division of labour that is a hallmark of the rise of market relationships over traditional ones (Braverman, 1974). In an increasingly capitalistic Altiplano, it is therefore unsurprising to see this new professional breed of totora cutters emerge. It is also not surprising that these men were from Huata, since that village enjoys quick and good road connections to Juliaca, which is the main market city in the Peruvian Altiplano. The only other person found in the entire study whose primary profession was cutting totora was in the town of Llachon, also in Peru, which has successfully transitioned to a tourism-based economy and has become a regular stop on tourist package holidays, and suggests how totora use may be maintained, at least marginally, through tourism long-term.

Conclusion

Implications of Totora Use on Traditional Ecological Knowledge

TEK is not static, and changes in uses of natural resources over time are inevitable, and undoubtedly the history of the use of totora from its first introduction to the region to the present day includes significant shifts. Our results suggest that there has been a decline in the use of totora driven by (global) economic forces. We do not envisage a reversal of these trends in the near future. This does not mean we think that totora will disappear from Lake Titicaca – the plant is not domesticated, and it appears to have increased in extent even as humans have come to rely on it less over the last 20 years (Villar et al., 2023). Nor do we expect people will cease to use and cultivate totora entirely. Smallholder animal husbandry will likely survive in some form in the region for decades and will likely continue to rely on totora for animal feed. The ecological consequences of the decline in totora harvesting are also difficult to predict, and totora burnings are no doubt harmful for bird species that nest in it (Villar et al., 2023; Pulido Capurro, 2018). However, the degree to which species of totora have become adapted to the human modified landscapes of totora wetlands is unclear. Work elsewhere in the world suggests that many seemingly wild biodiverse ecosystems rely on long-term human, generally indigenous, modification, to flourish (Bowman, 1998), and that the suppression or abandonment of those practices can be deleterious to biodiversity (Bliege Bird & Nimmo, 2018). Further ecological monitoring of the totora wetlands of Lake Titicaca is needed to understand the ecological consequences of this rapid change in human involvement with this landscape.

Our most significant finding is perhaps that the *ayllu* system of collective management of totora, which has existed for at least as long as there are written records for the region, has effectively been wiped out within a generation. This is not only a change of economic system but also represents a disruption of social bonds in the Altiplano on a scale unseen since early nineteenth-century attempts to enclose the commons. Given the reliance on human propagation of totora wetlands for most of their history in Lake Titicaca, there is also a question of whether this unique ecosystem that hosts significant numbers of endemic species can long survive without human aid, and what will happen if it fully disappears.

Parting Thoughts

Alles Ständische und Stehende verdampft – all that is solid melts into air. The use of totora as a staple plant in the area around Lake Titicaca dates back at least 4000 years, and the *ayllu* system to regulate it dates back at least 500. The *ayllu* survived the conquest of Pizzaro, the Bourbon Reforms, the Wars of Independence, and the various republics, dictatorships, revolutions, and civil wars which engulfed independent Peru and Bolivia – but it has not survived increasing market integration. While totora use has not disappeared, it has become more specialised. Market integration has undercut both totora harvesting through reducing the number of young workers available, totora goods by replacing them with cheaper manufactured ones, and the *ayllu* system by creating individual rather than communal economic actors. The full ecological, social, and cultural impacts of these changes are yet to be determined. For the totora one thing is clear - its role as a cultural keystone species is diminishing fast.

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Declarations

Ethical Approval This work received ethical approval from the Institutional Review Board of the Universidad Nacional del Altiplano, and University of Oxford's CUREC.

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The data used in this chapter can be found in Appendix B

6

Combining Modelling and Social Science Approaches to Understand Artisanal Fisheries Bycatch in Lake Titicaca

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Problems with combining modelling and social science approaches to understand artisanal fisheries bycatch

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Abstract

Aim: Artisanal fisheries account for 40% of the world's fisheries catch, yet its environmental impacts remain poorly understood. This is especially the case in developing countries. In this study, we sought to integrate Local Fisher's Knowledge with distribution modelling to estimate the annual bycatch of Titicaca Grebe (*Rollandia microptera*), an endangered endemic bird from Lake Titicaca whose main anthropogenic threat is bycatch.

Location: Lake Titicaca, Peru and Bolivia.

Methods: We conducted transect and point counts of fishing nets in March–September 2022 and conducted interviews with fishers across the Lake Titicaca region. Using bathymetry, distance from shore, distance from a settlement, distance from the protected area, presence/absence of aquaculture, distance from aquaculture, and wetland cover, we constructed a distribution model of fisheries using maximum entropy modelling. We conducted interviews with fishers asking about the frequency of grebe bycatch and conducted short-term monitoring at various sites while conducting transect points for dead grebes.

Results: We estimate 3270 km^2 of the surface area of Lake Titicaca is used for fishing, which amounts to 39.40% of the lake's surface area. The area under the curve (AUC) of the distribution model was 0.89 and the True Skill Statistic was 0.67, which suggests maximum entropy modelling can model fisheries occurrence. The results of our interviews suggested a biologically implausible large number of grebes caught as bycatch annually. The cultural context of the interviews, including potential influences of non-response and social-desirability bias, being with fishers who often view the Titicaca Grebe as a nuisance species, might have caused over-reporting of bycatch and hence led to these implausible figures.

Main Conclusions: It is possible to map fisheries using distribution models as one might with species. However, obtaining accurate measures of fisheries bycatch

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through interviews is more difficult, due to cultural factors which affect the accuracy in fisher's responses. While we hope that this method provides a low-cost alternative to monitoring, it is not a suitable replacement for it.

KEYWORDS
artisanal fisheries, Bolivia, bycatch, conservation social science, freshwater conservation, grebe, inland fisheries, Peru, small scale fisheries, waterbird mortality

1 | INTRODUCTION

The conservation of aquatic ecosystems is prone to having to rely on imperfect knowledge of fisheries, as monitoring is non-existent in many countries (Allan et al., 2005; Bartley et al., 2015; Lewison et al., 2014; Pelicice et al., 2021; Raby et al., 2011; Žydelis et al., 2013), and where monitoring does occur, crucial information which is of interest to conservationists and managers, such as bycatch rates, are often underreported (Bartley et al., 2015; Bremner et al., 2009; Luck et al., 2020). Artisanal fisheries, also called small-scale fisheries, defined as 'involving fishing households (as opposed to commercial companies), using a relatively small amount of capital and energy, relatively small fishing vessels (if any), making short fishing trips, close to shore, mainly for local consumption' by the Food and Agricultural Organization (FAO) of the UN (FAO, 2005), account for 40% of the global fisheries catch. Over 500 million people globally rely on artisanal fisheries, directly or indirectly, for their livelihood (FAO et al., 2023) and as the principal source of protein across many of the world's poorest regions (Bell et al., 2015; Heck et al., 2007). For these reasons, artisanal fisheries have received increasing attention from fisheries managers and biologists for several decades (Arthur et al., 2022; Lancker et al., 2019), recognising the importance of integrating artisanal fishers' knowledge into conservation programmes (Léopold et al., 2014; Psuty & Całkiewicz, 2021). But despite this, knowledge of the extent and impact of artisanal fisheries lags behind our understanding of commercial fisheries (Bartley et al., 2015; Raby et al., 2011; Žydelis et al., 2013).

Artisanal fisheries have occurred for nearly as long as humans have existed (Sahrhage & Lundbeck, 1992) and have had ecological impacts for just as long (Erlandson & Rick, 2010). Although artisanal fisheries are often more sustainable than commercial fisheries (Arthur et al., 2022), they can also lead to deleterious environmental impacts. Small-scale fisheries can lead to population declines due to overfishing (Allan et al., 2005; Gough et al., 2020), changes in community composition in fished areas (Hawkins & Roberts, 2004), and damaging bycatch of non-target species, such as amphibians, birds, and non-target fish (Barz et al., 2020; Psuty & Całkiewicz, 2021; Žydelis et al., 2009, 2013). These deleterious effects often increase as artisanal fishery fleets modernise, shifting from traditional nets to plastic monofilament ones (Orlove, 2002; Žydelis et al., 2013). Modern techniques can make fisheries more efficient and hence cause greater ecological impact, rendering previously sustainable fishing methods unsustainable (Campredon & Cuq, 2001; Orlove, 2002), in a manner analogous to how traditional hunting practices become unsustainable with the introduction of firearms for many traditional societies (Krech, 1999; Medinaceli & Quinlan, 2018).

Ignorance of the extent of, and ecological impact of, artisanal fisheries is especially extreme in the case of inland fisheries. Inland aquatic ecosystems are amongst the most threatened worldwide (Dudgeon et al., 2006; Reid et al., 2019; Strayer & Dudgeon, 2010). These are also the least studied ecosystems on earth (Dudgeon et al., 2006; Maasri et al., 2022) and are home to 9.5% of known species (Balian et al., 2008). Inland fisheries are an important economic sector and source of food in much of the developing world (Funge-Smith & Bennett, 2019), yet fishery management and conservation programmes generally fail to focus on inland ecosystems explicitly (Reid et al., 2019). The intensity and distribution of inland fisheries across most of the world are practically unknown (Allan et al., 2005; Funge-Smith & Bennett, 2019). No studies have managed to quantify rates of bird bycatch from inland artisanal fisheries (Raby et al., 2011); to our knowledge, only two studies, both in rivers, have mapped inland bycatch (Chiaravalloti, 2017; Xie et al., 2019). Given the paucity of monitoring and information on inland fisheries, it is of little surprise that official estimates have been found to underestimate inland fisheries fish catch by up to 60% (Fluet-Chouinard et al., 2018).

Here we present a case study from Lake Titicaca, where communities practise artisanal fishing in a highland closed basin, incorporating novel approaches to monitor their bycatch. We combine two methodologies which have long-established histories in conservation and ecology but which are rarely integrated within the same study to understand the spatial distribution of wildlife exploitation. These are species distribution models (SDMs) and ethnobiological techniques to extract fishers' local ecological knowledge.

SDMs have been developed and used in terrestrial ecology and conservation planning for over 30 years (Valavi et al., 2022) and have become a crucial part of the toolkit of many biogeographers, ecologists, and conservationists (Elith et al., 2006; Valavi et al., 2022). They have been used to map past ranges of ecosystems (Svenning et al., 2011), to estimate species ranges (Franklin, 2010) and abundances (Long et al., 2008), and have used a diversity of approaches depending on the information available and the questions being asked. SDMs have been used to model

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spatial relationships between environmental covariates used and the location and distribution of the object in question, including illegal logging (Barber-Meyer, 2010), settlement patterns of prehistoric humans (Demján et al., 2022), and poaching intensity (Moore et al., 2018). In biology, SDMs are especially useful for studying elusive and rare species and species that lack long-term and consistent monitoring programmes, since they allow conservation practitioners and ecologists to make predictions based on limited data (Stockwell & Peterson, 2002).

In the context of fisheries, many studies have used catch data to model species distributions (Paradinas et al., 2023; Pennino et al., 2016) or fishing intensity for those species, usually based on consensus expert opinion of drivers of fishing intensity (zu Ermgassen et al., 2020), and several studies have applied distribution modelling techniques developed to map species ranges to study fisheries occurrence (Crespo et al., 2018; Griffin et al., 2021; Stock et al., 2020). However, neither previous study used SDMs to study either artisanal fisheries or inland fisheries, which are the ones most lacking in information. We believe that artisanal inland fisheries are potentially analogous to poorly monitored species as objects with a non-random spatial distribution which has movement constraints on its location, within a range that is constrained by spatially explicit environmental covariates. Here we present an example from Lake Titicaca of how SDMs can be used to model inland artisanal fisheries, their catch, and their bycatch and discuss potential applications of this approach for conservation planning and ecology.

While distribution models are important for establishing the spatial distribution of fisheries, they do not in themselves tell us the extent of fisheries bycatch. Traditionally, most studies of fisheries bycatch have relied on either monitoring by on-deck researchers (e.g. Forget et al., 2021) or combining monitoring of selected vessels with legally mandated logbooks (e.g. Gerritsen & Lordan, 2011). However, neither of these methods is plausible in the context of artisanal fisheries in developing countries, where fishers do not keep logbooks and vessels are often too small to carry extra people. Instead, we rely on the local ecological knowledge of fishers themselves to help understand the extent of fisheries bycatch in these artisanal fishing systems. While many branches of ecology and conservation science are only recently beginning to understand the importance of local ecological knowledge (LEK) and traditional ecological knowledge (TEK) (Joa et al., 2018; Molnár & Babai, 2021; Thomsen et al., 2023), fisheries science has been incorporating both of these into its scientific research for decades (Castagnino et al., 2023; Johannes et al., 2000), including in studies of fisheries bycatch (Léopold et al., 2014; Psuty & Całkiewicz, 2021). There are many ways to integrate LEK and TEK into ecological studies, but one of the most common is through interviews (Newing, 2011). Interviews are considered the best and most cost-effective manner of estimating fishery intensity and fishery bycatch in artisanal fisheries where long-term monitoring of observation programmes is not a viable option (Karris et al., 2013; Moore et al., 2021; Szostek et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Study site and fieldwork

The data for this study come from surveys of Lake Titicaca (Figure 1), in Peru and Bolivia, between March and September 2022. Based on our own observations, previous anthropological work on Lake Titicaca fisheries (Orlove, 2002), and knowledge of the area, we cannot discern a seasonal pattern in fishing effort and thus do not take seasonality into account for our model. Furthermore, there have been no studies on the movement ecology of the Titicaca Grebe, including any potential seasonal variations in foraging behaviour, making it impossible to integrate seasonal differences in their movement into our model. Lake Titicaca is the world's highest-altitude navigable lake, with a surface altitude of 3812 m (Dejoux & Iltis, 1992). It is home to a number of endemic aquatic species that are thought to be threatened by overfishing and fishery bycatch, including the endangered endemic Titicaca Grebe (*Rollandia microptera*), Titicaca Giant Frog (*Telmatobius coleus*) and 28 species of endemic killifish of the genus *Orestias* (Lauzanne et al., 1992; Martinez et al., 2006; Vellard & Dejoux, 1992; Vila et al., 2007; Villar et al., 2023), though this might be an underestimate, given the relative lack of knowledge of the lake's fauna. Lake Titicaca is considered a hotspot for neotropical freshwater endemism, since 92% of the fish species are endemic (Albert et al., 2011). Lack of information on the occurrence of fisheries in Lake Titicaca has been cited as a significant barrier to conservation in the region (Martinez et al., 2006) and as a barrier to sustainable fishery management in Lake Titicaca (Vera Cartas et al., 2013; Villwock, 2001).

Fishing has occurred in Lake Titicaca for millennia (Capriles et al., 2014; Erickson, 2000), but for most of the history of human habitation, fishing was a relatively rare activity, associated with periods of environmental and political instability (Miller et al., 2021; Young, 1997). Anthropological evidence suggests that fishing was considered a low-status profession until the mid-20th century, since it was associated with landlessness and was thus generally undertaken by the lower status Uro ethnic group (Forbes, 1870; La Barre, 1941, 1948). The introduction of commercially important salmonids (*Salmo* sp.) and pejerrey (*Odontesthes bonariensis*) between the 1930s and 1950s significantly changed the economics of fishing in the lake. Previously agricultural communities began commercial fisheries, leading to a fishing boom in the 1960s. This boom crashed due to declining prices of trout in the 1970s (Bouysse-Cassagne et al., 1992; Everett, 1973; Laba, 1979), but fishing has remained a staple of the rural economy of the Lake Titicaca region. In the 1990s, it was estimated that roughly 3000 individuals worked as fishers on Lake Titicaca (Bouysse-Cassagne et al., 1992), but there have been no surveys done since then. Many fishers report drastic declines in catch over the last decade (D. A. V., pers. obs.), and there has been an increase in aquaculture in Lake Titicaca at the same time, characterised by fish farms in the lake itself, primarily focused on breeding trout for commercial sale. Lake Titicaca is home to the Reserva

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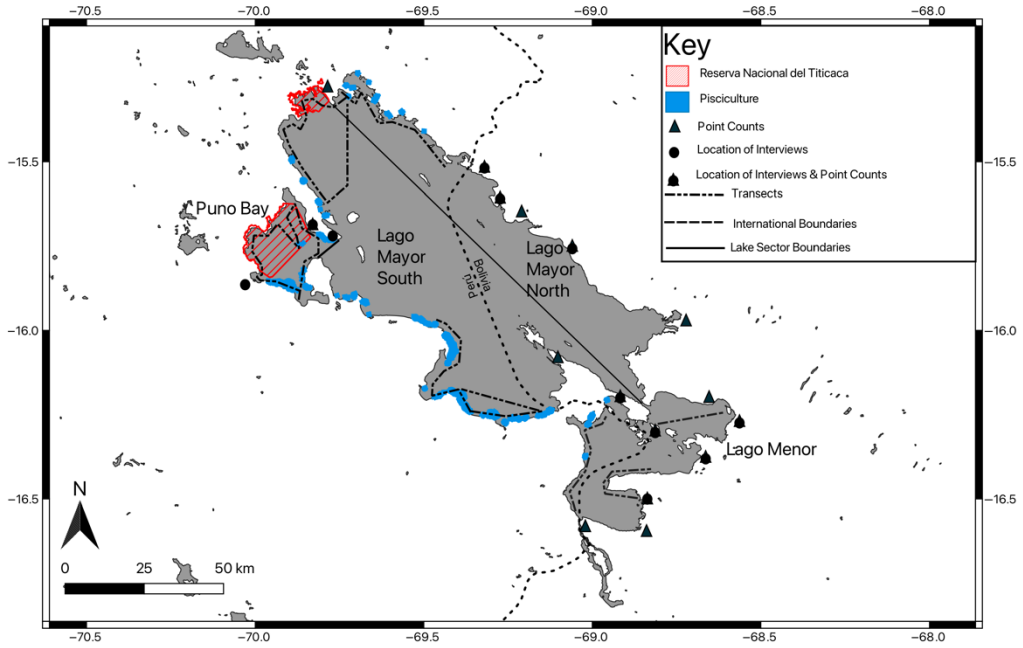


FIGURE 1 Map of Lake Titicaca, with sectors of the lake and transect routes labelled.

Nacional del Titicaca, within whose boundaries fishing is theoretically banned for all save certain individuals with traditional usage rights, but this prohibition is regularly flouted.

Nets were counted alongside birds during transects and point counts. The fishers on Lake Titicaca use monofilament nets, which are left in situ overnight. They are weighed down by stones on the bottom and have cork tied to the top to keep them horizontal in the water. Each net has a longer line tied to the end of it, at the end of which is generally a large disused plastic bottle, which is used by fishermen to find them again. It is these tied-up plastic bottles that are counted to estimate net numbers. Historically, there were also nets made of plant fibre in Lake Titicaca (Orlove, 2002), but we found no evidence of their use, and only scarce evidence of anyone under 60 being aware that local plant fibres could be used to make nets. Point counts were made from the shore, and transect counts were made from fishers' boats. Information on the time, length, and location of the transects and point counts can be found in the Supplementary Materials. GPS coordinates were taken of the locations of the counts. There were a variety of observers involved in counting nets, but all counts included D. A. V. All counts had at least two observers. Locations for transects were based on where local fishers were willing to rent the research team their boat for the day and how far their boats could travel. Surface counts of nets are considered accurate since the main form of fishing in Lake Titicaca is to place nets near the surface of the lake, with empty plastic bottles as floats. Abandoned nets were also counted as for logistical reasons they could not be differentiated from active nets. We do not expect that net abandonment follows a specific geographic pattern, as fishers usually abandon nets out of failure to find them again, rather than intentionally (pers. obs.). Abandoned nets would also produce bycatch which is, by definition, unreported by any interview or survey. While net length varies, the standard length of individual nets in most areas of Lake Titicaca is 100 m as sold in the cities of El Alto and Juliaca, the two major centres of commercial activity in the Altiplano in Bolivia and Peru, respectively (pers. obs.).

2.2 | Environmental variables

We used bathymetry, distance from shore, distance from a settlement, distance from the Reserve National del Titicaca, presence/absence of aquaculture, distance from aquaculture, and wetland cover as environmental variables for our distribution model. Points within the Reserva Nacional del Titicaca had a value of 0. Before running further analyses, we tested collinearity of all variables using the Variance Inflation Factor (VIF) (Akinwande et al., 2015). A VIF greater than 10 indicates a problem of collinearity within a model (Chatterjee & Hadi, 2006) and is generally accepted as the cutoff for removing variables in SDMs (Naimi et al., 2014). VIF analysis was done in R version 4.3.0, using the usdm package (Naimi et al., 2014).

We chose variables which we considered most likely to influence the presence of fishing in an area. Distance from settlement was

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chosen since interviews with fishers suggest that time from the dock is an important consideration for where they lay their nets. Distance from shore and bathymetry were chosen for similar reasons; fishers in Lake Titicaca often cannot swim and rarely carry life jackets (pers. obs.), and it was unclear to us whether water depth or distance from shore was more important in establishing, for themselves, which areas are considered too dangerous to lay nets. Distance from the Reserva Nacional del Titicaca was chosen since the reserve is meant to be an area where fishing, while allowed for some individuals with customary usage rights, should be restricted, and to test if it was being effective as a protected area. We were unsure how to measure aquaculture, as both presence of aquaculture (Cheng et al., 2022) and distance from aquaculture (D'Amours et al., 2008) have been found to influence distributions of aquatic species and have been known in some regions to replace fishing as fish stocks decline (Longo et al., 2019). Unfortunately, the effect of aquaculture in general on wildlife, especially in inland contexts, remains understudied (Barrett et al., 2019), making it unclear whether presence/absence or distance should be the standard method of studying its effects. We therefore included both. We included wetland cover since many fishers lay their nets parallel to the edge of wetlands to catch fish moving in and out of them for shelter.

Bathymetry data were obtained from an internal bathymetric map made by the Autoridad Binacional Autónoma del Sistema Hídrico del Lago Titicaca. The borders of Lake Titicaca used to make the distance from shore raster were obtained from the HydroLakes lake polygon dataset (Messager et al., 2016). Distance from the Reserva Nacional del Titicaca was calculated using the official polygon of the reserve boundaries of the Reserva Nacional del Titicaca from SERNANP (2023). Data on the location of settlements to create the distance from the population centre raster were obtained from the WorldPop Dataverse repository, using unconstrained 100 m × 100 m data (Lloyd et al., 2017). Percentage wetland cover is from Villar et al. (2023). Aquaculture data are from satellite imagery of Lake Titicaca. All rasters were cut to the extent of Lake Titicaca and have a resolution of 1 km × 1 km. This resolution was chosen as it was the resolution of the lowest resolution environmental layer, namely the bathymetric map of the Autoridad Binacional Autónoma del Sistema Hídrico del Lago Titicaca.

2.3 | Fisheries distribution models

For the fisheries distribution model, we used maximum entropy modelling (MaxEnt; Phillips et al., 2006), a widely used model which uses presence data and pseudo-absences, and which has been shown to be amongst the most reliable and robust methodologies for estimating species distributions across a variety of situations (Elith et al., 2006; Valavi et al., 2022) including for aquatic species (Robinson et al., 2017). Maxent has been found to be particularly robust for modelling distributions of species where very little is known a priori of drivers of distribution (Radomski et al., 2022). The output of such a model is a probabilistic map of the occurrence of the modelled object. We used 1000 pseudo-absence points in our analysis. To correct for geographic sampling bias, we used a Gaussian density kernel model bias file to weight the position of pseudo-absence points (Elith et al., 2010). The model was run 100 times, each time withholding a random 30% of the dataset as a test set using a subsampling method to validate the model. We estimated the total number of nets following the logic of Long et al. (2008), Mladenoff and Sickley (1998), and Villar et al. (2023), which assumes that the density of what is being modelled is constant across the suitable range. This permits us then to estimate the total number by multiplying the average density of nets in the area observed by the total area predicted to have nets, the latter being defined by the binary map. 95% confidence intervals for the population are derived from the standard error of the observed density counts. As the pixel size in our rasters is 1 km × 1 km, density measured in km^2 is equivalent to density per pixel. Net density comes from the effective range of the binoculars used in these surveys. In the experience of the authors, nets cannot be identified at a distance of more than 500 m using 8 × 42 binoculars. We therefore assumed the area surveyed on the basis of 500 m from the observer for point counts and 500 m in either direction, totalling 1000 m, in the case of transects.

To validate the models, we used the average Area-Under-the-Curve (AUC) and True Skill Statistic of the 100 runs of the model. These are two commonly used metrics for model performance, with an AUC of over 0.8 or a TSS of over 0.5 considered to indicate a good model fit (Allouche et al., 2006; Komac et al., 2016). To convert the continuous probabilistic map of occurrences of fisheries into a binary map which could be used by the lowest presence threshold (Phillips et al., 2006), which assumes that all locations with a greater probability of the presence of the object being modelled, in this case fisheries, is suitable for the presence of the object being modelled. SDMs were constructed in R version 4.3.0, using the sdm, terra, sf, and raster packages (Hijmans et al., 2023; Hijmans et al., 2024; Naimi & Araújo, 2016; Pebesma, 2018). Figures were made using the package ggplot2 (Wickham, 2016) and in QGIS.

2.4 | Interviews

A disadvantage of counting nets from the surface is that it ignores the differences between nets meant to catch smaller fish, such as ispi (*Orestias ispi*), and those meant to catch larger fish, such as pejerrey. These nets not only catch different types of fish but are expected to catch different types of bycatch. As part of a broader ethnobiological study of the Altiplano region (Quispe et al., 2023; Villar, Thomsen, Gutiérrez Tito, et al., 2024; Villar, Thomsen, Paca-Condori, et al., 2024; Villar, Yanes, Gutiérrez Tito, & Gosler, 2024), fishers took part in semi-structured interviews which asked about what fish they targeted, the size and length of their nets, and about fishery bycatch. Before being asked about the Titicaca Grebe or bycatch, fishers were shown photographs of the Titicaca Grebe, in order to ensure that they were answering questions about the correct species. Interviews lasted anywhere between 20 min and 2 h. Interviews occurred during the same time period as the counting of nets. Responses of grebe bycatch were standardised to be per month and by the number of

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nets that fishers claimed to use. Full details of interview methodology can be found in Villar, Thomsen, Paca-Condori, et al. (2024). Ethical approval for surveys was obtained from the University of Oxford and the Universidad Nacional del Altiplano.

2.5 | Integrating model and interview results

We divided Lake Titicaca into four regions: the Lago Menor, Northern Lago Mayor, Southern Lago Mayor, and Puno Bay (Figure 1). Lago Menor and Puno Bay are both well-defined sub-regions of Lake Titicaca, while Northern Lago Mayor was separated from Southern Lago Menor by a line from the Straits of Tiquina to the Mouth of the Ramis River. We ran an interview-based model, which extrapolated the amount of bycatch in each net type based on interviews with fishers, using the logic of Moore et al. (2010), which assumes that fishers are honest is describing the frequency of grebe bycatch. Because fishers were permitted to answer the interviews of bycatch using any time interval they preferred, their answers were averaged to be over the course of a month. The standard length of a net in the region is 100 m (D. A. V., pers. obs.); however, some fishermen reported using nets of different lengths, such as 50 or 150 m. We standardised the number of nets which each fisher had to be the number of 100 m lengths of net. To compare whether the different regions of the lake reported different fisheries bycatch, we used the Kruskal–Wallis test (Kruskal & Wallis, 1952). We then got the annual estimate of fisheries bycatch by the following equation: $B = (A * (N * I)) * 12$. B is annual bycatch, A is the total area where we expect there to be fisheries as per the binary fisheries raster described above, N is the observed density of nets per km^2, I is the average of fishers' interviews' estimated grebe bycatch per net per month, and 12 is the number of months in the year. We also ran a model based on monitoring described below.

2.6 | Monitoring fisheries

Due to the limitations of the fieldwork, researchers were not in villages over long periods of time and we were therefore unable to establish a long-term net monitoring programme that would detect relatively rare events such as grebes being caught as bycatch. We used these monitored numbers to provide a rough estimate of grebe mortality from bycatch independent from the interview results, which will in part account for the documented inaccuracy of fishers' own accounts of bycatch in other regions (Bremner et al., 2009; Kennelly, 2020; Mucientes et al., 2022). Each morning we located fishers returning from their nets and shaking out their contents. We also searched for dead grebes near piers and other sites which are known to be used by fishers for docking; grebes found that appeared fresh and showed signs of drowning or strangulation were assumed killed as bycatch during the monitoring period. We then extrapolated the number of dead grebes from these surveys to estimate grebe death numbers across the areas classified as with high probability of fishing by MaxEnt, using the formula $\left(\left(\frac{G}{D*V_O}\right)*365\right)*V$, where G is the number of dead grebes, D is the number of days spent in the field, V_O is the number of observed villages, and V is the number of settlements where fishing is a significant economic activity. According to the latest estimate of the demographic of fisheries across the Altiplano, it is estimated that fishing is a significant economic activity in 151 villages in Lake Titicaca (Orlove et al., 1992). 365 refers to the number of days in the year.

2.7 | Sensitivity analysis

Each of the models used to estimate fisheries bycatch rates across Lake Titicaca relied on a number of assumptions, many of which cannot be tested directly. To look at the robustness of the models we used, we used sensitivity analysis. Sensitivity analysis has developed a branch of statistics to measure the sensitivity of models to changes in input parameters and to study the contribution of uncertainty in different parameters to the global uncertainty of the model (Frey & Patil, 2002). Most sensitivity analysis is probabilistic, assuming paired dependent and independent variables; however, probabilistic sensitivity analysis is not appropriate for evaluating the models used in this study to estimate fisheries bycatch because they are deterministic. We therefore used deterministic sensitivity analysis, a branch of sensitivity analysis widely used in economics (Vreman et al., 2021) and in systems biology (Simoni et al., 2020), but rarely used in ecology.

We ran sensitivity analysis on two models: one based on our observations of dead grebes and one based on interviews with fishermen. The model based on our observations of dead grebes is written above, but to recap, it is $B = \left(\left(\frac{G}{D*V_o}\right)*365\right)*V$, where G is the number of dead grebes, D is the number of days spent in the field, V is the number of settlements where fishing is a significant economic activity, and B is the total yearly bycatch. We tested the robustness of our model relative to variation in V, the number of villages where fishing is a significant economic activity. This is because the last datapoint we have for this number is a generation old (Orlove et al., 1992), and neither the Peruvian nor Bolivian census collects information necessary to determine how many villages exist where fishing is a significant economic activity. Any variation in this variable used in our analysis would have to be arbitrary, so we bounded the reasonable variation in V by double 151, or 302, and half of 151, or 75.5.

The model used to integrate the distribution model with fishers' answers to estimate global grebe bycatch is $B = (A * (N * I)) * 12$ (model components as stated above). The upper and lower bounds of the N and I came from the 95% confidence interval of the observed values. If the data are over-dispersed, this could go below 0, which is logically impossible for net density or fisheries bycatch. If the lower bound goes below 0, the lower bound used for sensitivity was set to 0.1 as an arbitrary value. For A, the upper and lower bounds were set using the same thresholding method as described above, but rather than using a threshold of 1, where the least suitable habitat was the least suitable one found model, the lower bound was the point in the 75th percentile of suitability for fishing, and the upper bound assumes that habitat which had 25% less chance of being suitable for fisheries

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could still have fisheries within it. The 75th percentile of suitability is a commonly used arbitrary threshold for converting continuous distribution models to binary presence/absence maps (Liu et al., 2013).

In addition to these methods, we also looked at the effects of outliers on our dataset. To test whether our data on either net counts or fisher's response to the frequency of grebe bycatch included outliers, we used Grubbs' test (Grubbs, 1950) to determine if the lower or upper bound of each of these datasets were outliers. Following the recommendation of Benhadi-Marín (2018) in cases where extreme values were found to be outliers, they were dropped. This was repeated until no outliers remained. The aforementioned models to estimate bycatch and to study the sensitivity of the model were re-run without outliers. The analyses in this section were conducted in R version 4.3.0, using the *outliers* package (Komsta, 2022).

3 | RESULTS

3.1 | Fisheries extent and field results

We counted a total of 1128 nets over the course of 36 point counts and 115 transects, including repeated surveys. Sixteen point counts and 3 of the transects were in Bolivia, and 112 transects and 20 of the point counts were in Peru. The aforementioned environmental variables all had a VIF of under 10, so we proceeded to do the analysis using all the variables described above. Assuming a 500 m effective range of the binoculars, our surveys showed an average net density of 3.84 ± 6.48sd per km^2, excluding those surveys where no nets were found.

In total, 54 fishers gave quantitative estimates in interviews of the amount of bycatch: 25 in Lago Menor, 13 in Northern Lago Mayor, 13 in Puno Bay, and 3 in Southern Lago Mayor. Across the entire lake, the average reported bycatch per net per month was 0.908 ± 2.136sd grebes. In Lago Menor, reported bycatch was 0.404 ± 0.710sd; in Northern Lago Mayor, it was 0.600 ± 0.730, in Puno Bay it was 2.280 ± 3.978; and in Southern Lagor Mayor, it was 0.483 ± 0.559. We found no significant difference in the self-reported grebe bycatch levels per net per month across the different zones of Lake Titicaca ($\chi^2 = 7.361$, df = 3, $p = 0.061$).

The distribution model averaged an AUC of 0.89 and a TSS of 0.67 across its 100 runs, indicating a good fit to the data. By use of the binary model, we estimated that 3270 km^2, or 39.50% of the lake surface (Figure 2), was used for fisheries, with the threshold being a 4.963% chance of the pixel being suitable for fisheries, that being the lowest presence threshold. The environmental variable contributions to the dataset were, in descending order, distance from the shore (34.4%), bathymetry (19.5%), distance from protected areas (9.6%), distance from pisciculture (7.8%), totora

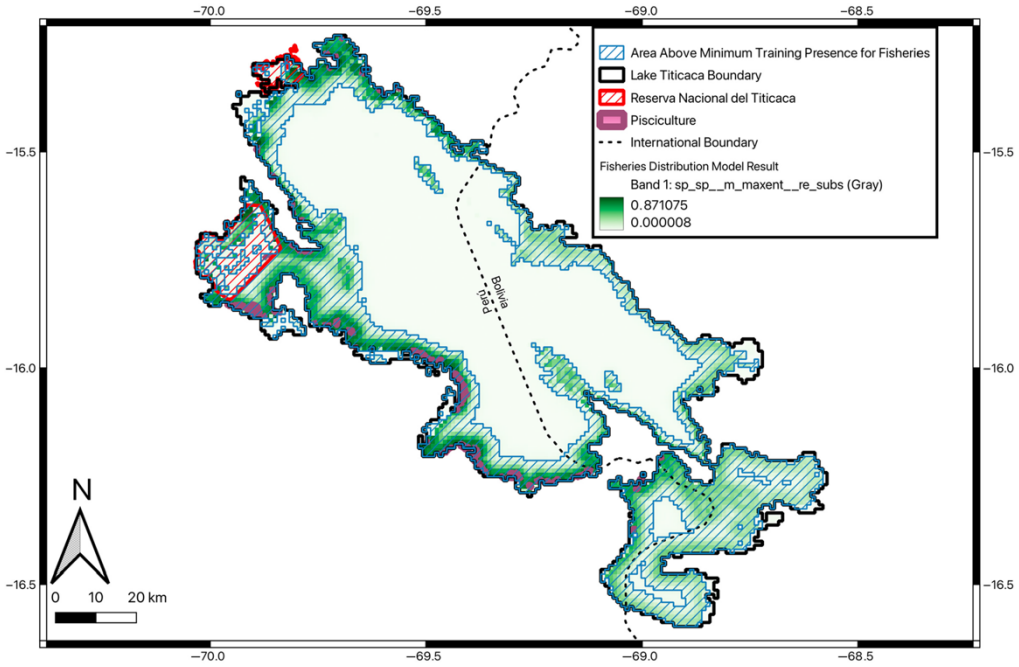


FIGURE 2 Map of distribution model results. Areas in hatched blue are above the lowest presence threshold used to convert the continuous distribution model results to a binary result, and areas hatched in red are within the Reserva Nacional del Titicaca.

presence (4.1%), distance from settlements (4%), and presence/absence of pisciculture (0.3%).

Over 6 months of fieldwork, we visited 23 sites, out of an estimated 151 settlements which engage in fishing (Orlove et al., 1992). In total, 85 days were spent in the field during monitoring. We found a total of 29 dead grebes over the course of this fieldwork. We also found several other waterfowl species being caught as bycatch, including the Andean Ruddyduck (*Oxyura ferruginea*) and Rolland's Grebe (*Rollandia rolland*), as well as evidence of the Titicaca Giant Frog being caught as bycatch.

3.2 | Bycatch estimation

As we found no difference in the self-reported levels of bycatch between the regions of Lake Titicaca, we used the average reported bycatch of the entire lake to estimate bycatch rates. Upper and lower estimates of possible bycatch across the lake based on our above-described sensitivity analysis are given in parenthesis, while full results in variation of possible bycatch are shown in Figure 3. Bycatch numbers are given to the nearest whole number. Based on our observations of grebe bycatch, we estimated a lakewide total annual bycatch of 648 (324–1297) individuals. Based on our interviews with fishers and our distribution modelling, we estimate a potential bycatch of 189,474 (61–3,669,555) individuals per year. The bulk of the variation came from A, or the area used for fisheries, in our model (Figure 3). This appears to be the case because many fisheries occur in territory which is just above the threshold set for converting our continuous model results to a binary result. However, given the subsistence nature of the Altiplano economy, and the tendency of the local Aymara people to use all available territory for economic activity, we consider it unlikely that there is much territory which could be used for fishing but remains unutilised, or territory which is used for fisheries which doesn't yield fish.

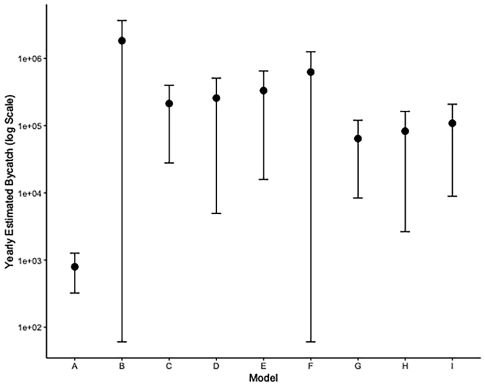


FIGURE 3 Estimates of Yearly Grebe bycatch from all models used in this study. (A) Estimated bycatch from researcher observations. (B) Global interview and GIS-based model which includes outliers, (C) bycatch estimation varying only area fished, (D) Bycatch estimation varying only net density, (E) bycatch estimation varying only interviewee responses, (F) global bycatch estimation excluding outliers, (G) bycatch estimation varying only area fished outliers excluded, (H) bycatch estimation varying only net density outliers excluded, and (I) bycatch estimate varying only interviewee response outliers excluded.

Grubbs' Test found that six of our counts had outlier net densities. These were transects where the net density was observed to be 35.794, 33.606, 11.891, 11.094, 11.073, and 9.066 nets per km^2. Of these, two were in Lago Mayor South, three in Lago Mayor North, and one in Lago Menor. One fisher's response was an outlier, a fisher in Puno who reported capturing an average of 15 grebes a month as bycatch. Excluding these outlying figures, we estimated average net density at 2.153 ± 2.04sd nets per km^2 and reported bycatch at 0.642 ± 0.870sd individuals per month. Removing the one interview outlier made no difference to the reported bycatch rates ($\chi^2 = 5.874$, df $= 3$, $p = 0.118$), so we continued to use lakewide averages in our estimates. Excluding these outliers, we estimate a total of 57,025 (60.72–1,253,819). Once again, we found that the model was highly sensitive to the area of the lake considered suitable for fisheries and the estimated net densities (Figure 3 model F).

4 | DISCUSSION

Grebe bycatch per net did not appear to differ significantly by geographic area across Lake Titicaca. However, the SDM suggests that Lago Menor should be the focus of anti-bycatch activities in the Lake Titicaca region, as it is the lake sector with the percentage of area considered suitable for fisheries by the distribution model. It also suggests that since most areas with predicted fisheries are within 2 km of the coast, and fishing is chiefly concentrated near the lakeshore, fishery distribution is largely restricted to coastal areas.

All estimates of grebe bycatch suggest that it is a major problem for the long-term conservation of the Titicaca Grebe. However, the figures from the interviews are impossibly high, even when accounting for outliers. BirdLife International estimates there to be fewer than 1000 Titicaca Grebe individuals alive (BirdLife International, 2020). While we have reason to believe that this is a significant underestimate (Villar, Velásquez-Noriega, Gutiérrez Tito, et al., 2024), the grebe bycatch estimated here is still significantly higher than the total population estimated from our surveys of the Titicaca Grebe. The Titicaca Grebe is clearly not extinct, so what remains is to account for this discrepancy. The results from villages might be biased by incorrect assumptions at various points. There has been no general survey of fisheries of the Lake Titicaca region since the figure of 151 villages relying on it was published (Orlove et al., 1992), but anecdotal evidence suggests that the number of fishers has declined since then. The use of other resources from Lake Titicaca, such a totora and a sedge, has also declined since then Villar, Thomsen, Gutiérrez Tito, et al. (2024), and in many fishing villages, primarily

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older residents remain (pers. obs.). We also could not correct for differences in the number of fishers across these 151 villages, since Orlove et al. (1992) did not provide a list of them against which we could work, nor has there been an effort subsequently to quantify the number of fishing villages, or active fishers in Lake Titicaca. We might also have assumed incorrectly how long it took for a grebe to decompose in the Altiplano. We only counted grebes which looked relatively fresh, with no signs of decay. However, in the dry conditions of the Altiplano, these individuals may have been killed earlier than on the day on which they were found by researchers. A field experiment measuring time of decomposition would be required to test how accurate was this assumption. Discrepancy in interviewee answers compared with biologically plausible numbers of grebe bycatch deaths might reflect the negative attitude of many fishers, who regard the grebe as a problem species (Quispe et al., 2023; Thomsen et al., 2023; Villar, Thomsen, Paca-Condori, et al., 2024). Thus the excessive number of dead grebes might be either a form of boast, of having killed so many individuals of a species they dislike, or a rationalisation of their dislike for the grebe, so exaggerating the damage that the grebe does to their nets. This would be similar to how exaggerated claims of damage from wolves have been used to justify scientifically unnecessary culling programmes (Vucetich & Nelson, 2017). Possible structural weaknesses of the questionnaire-based survey, e.g. incorrect identification of the Grebe species accidentally trapped in nets, might also have caused over-reporting of bycatch of Titicaca Grebe by local fishermen, and hence led to these implausible outcomes.

Results from researcher observations of dead grebes in surveyed villages indicate a more plausible bycatch rate of 648 individuals a year. While the IUCN states that there are likely to be fewer than 1000 Titicaca Grebes left (BirdLife International, 2020), our estimates indicate that the population might be closer to 12,000 (Villar, Velásquez-Noriega, Gutiérrez Tito, et al., 2024). This would indicate that fishery bycatch is still a significant threat to the Titicaca Grebe and should be the focus of future conservation efforts. However, the fact that our relatively sparse observations conducted over a large number of villages give an estimate which seems more plausible than a method which combines GIS and LEK indicates to us the importance of standardised bycatch monitoring. The 648 estimate should be considered just the first rough attempt to quantify a problem which has been identified as a threat to this species for decades (O'Donnell & Fjeldså, 1997; Martinez et al., 2006). Further monitoring, over longer timeframes and in more settlements, is needed to provide a more accurate estimate of the annual mortality of the Titicaca Grebe to fisheries bycatch.

The total number of grebes caught as bycatch reported from interviews with fishers in this paper is almost certainly an exaggeration. While our results do not but provide a first attempt at estimating annual fisheries bycatch of the Titicaca Grebe, our research has confirmed that fishery bycatch remains a significant problem for the conservation of the Titicaca Grebe. The current study also highlights the urgent need for updating information on trends and population size of the target species, given that most recent estimates give the population as either under 1000 individuals (BirdLife International, 2020) or between 1000 and 2000 (Harrison et al., 2021), so as to evaluate in a more robust way the possible threats for its conservation, such as bycatch mortality. We have also shown that distribution modelling can be used to study the geographic extent of artisanal fisheries and that Local Fishers' Knowledge (LFK) is unlikely to provide reliable bycatch estimates for other species of conservation concern in Lake Titicaca such as the critically endangered Titicaca Giant Frog (Angulo, 2008). While we do not dispute that LFK can be useful in establishing conservation programmes in other situations (Johannes et al., 2000; Martins et al., 2018), and indeed may be useful for some elements of conservation in Lake Titicaca, it has proven unreliable to study the impact of fishery bycatch on the Titicaca Grebe population. Like any other source of information, LFK has to be used critically, and the cultural context of fishers' responses has especially to be considered when incorporating the information they report into conservation planning and ecological studies. We therefore suggest setting up long-term net monitoring, which would require training fishers to monitor nets. While this is more expensive than conducting interviews, it is probably the only method sustainable in the longer term to obtain accurate estimates of bycatch in Lake Titicaca. We also recommend that bycatch prevention and mitigation programmes should be implemented in Lake Titicaca, since even if the exact scale of the problem of bycatch remains unknown, it is clear that it is a significant conservation issue in this ecosystem. This could be asking fishermen to bring GPSs to the field and the time when they place and collect nets, to be able to get fine-grained information on the biogeography of Grebe bycatch in Lake Titicaca, experimenting with nets of different colours and widths, and placements of nets at various depths.

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CONFLICT OF INTEREST STATEMENT

We are not aware of any conflict of interest in this research.

DATA AVAILABILITY STATEMENT

Data is available in the Dryad link 10.5061/dryad.vt4b8gtzz.

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BIOSKETCH

Daniel A. Villar is a DPhil candidate at the Department of Biology, University of Oxford, with a thesis focused on the ecology and conservation of the Titicaca Grebe (*Rollandia microptera*).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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The data used in this chapter can be found in Appendix B

7

Addressing conflict between fishermen and the Titicaca Grebe (*Rollandia microptera*) through diet analysis

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Short Communication

Addressing conflict between fishermen and the Titicaca Grebe (*Rollandia microptera*) through diet analysis

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Human–wildlife conflict is often a driver of species declines, and understanding the material basis of this conflict is the first step in addressing it. The Titicaca Grebe *Rollandia microptera* is an endangered endemic species found solely in the Lake Titicaca watershed of Peru and Bolivia, and has experienced population declines due to fisheries bycatch. Human fishers often have negative opinions of the Titicaca Grebe, because they consider it as a competitor for declining fish stocks. We tested that assumption by an analysis of the bird's diet and found that the Titicaca Grebe does not compete with fishers for more lucrative fish species such as trout *Oncorhynchus* sp. and Pejerrey *Odontesthes bonariensis*, but does compete for the less desirable (to human fishers) native *Orestias* sp.

Keywords: diet, grebe, human–wildlife conflict, piscivore, stomach contents.

Human–wildlife conflict is a significant driver of population declines of species the world over (Nyhus 2016). Although human–wildlife conflicts can have many causes, a common one is when animals predate on species in which humans have an economic interest. Usually, this is livestock (Plumer *et al.* 2018, Jacquier *et al.* 2020), but in marine and aquatic species, conflict often stems from wild animals predating on other wild animals that are the target of human fisheries (Guerra 2019, Hoel *et al.* 2022). Perceived conflict with wildlife can be as much of a barrier to conservation as actual conflict (Guerra 2019), and knowledge of the empirical unreality of conflict is often not enough to reduce human–wildlife conflict (Treves *et al.* 2013), but knowledge of the source and extent of conflict is a necessary first step towards mitigation (Toomey 2023). Without knowing the actual basis of the conflict between humans and wildlife, any conservation actions are based purely on hunches, rather than science. Knowing the extent of conflict can also indicate whether education campaigns informing humans that conflict is primarily imaginary can be run, as well as suggesting what behaviour modifications can be reasonably expected of humans.

The Titicaca Grebe *Rollandia microptera* (hereafter referred to as Grebe) is an Evolutionarily Distinct and Globally Endangered (EDGE) species (Jetz *et al.* 2014), endemic to Lake Titicaca and associated water bodies in Peru and Bolivia (Fjeldså 2004, Llimona *et al.* 2020, Villar *et al.* 2023). The Grebe, which is flightless, saw a population decline of around 70% between the 1970s and the early 2000s (Engblom *et al.* 2001). This decline could have multiple causes, including changes to the Lake Titicaca ecosystem caused directly by the introduction of salmonids, but is thought to be primarily driven by mortality due to fisheries bycatch (Martinez *et al.* 2006). However, there is widespread animosity amongst fishers towards the Grebe, because it is seen as competing directly for fish (Quispe *et al.* 2023, Villar *et al.* 2024a). This study aims to find the material basis of this perceived conflict, and then make conservation recommendations on the basis of this material basis. We do not pretend that knowing the extent of dietary niche overlap will resolve conflict between fishers and Grebes and will immediately reduce Grebe bycatch. However, knowledge as to whether this dietary niche overlap is real or imagined can inform what sort of environmental education campaigns should be run to foster Grebe–fisher coexistence, as well as inform whether changes in fishing patterns are likely to be effective at reducing Grebe bycatch. In the latter case, if Grebes and fishers are indeed targeting the same fish species, then it is not reasonable to expect fishers to change where they fish, but it might be possible for them to use visual cues, such as thicker nets, that reduce bycatch while not reducing fisheries catch.

The introduction of fish, especially salmonids, has been associated with the extinctions of at least three species of endemic grebes in the 20th century, the Alaotra Grebe *Tachybaptus rufolavatus*, the Colombian Grebe *Podiceps andinus* and the Atitlan Grebe *Podilymbus gigas* (LaBastille 1983, Fjeldså 1993, Wilmé 1994,

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O'Donnell & Fjeldså 1997). In Lake Titicaca, salmonids *Oncorhynchus* sp. and Pejerrey *Odonesthes bonariensis* were introduced in the mid-20th century (Everett 1973, Laba 1979, Lauzanne *et al.* 1992). The specific causes differ between these species. In some cases, invasive salmonids eat macrozooplankton, depleting either the diet of the Grebe directly, or reducing the number of fish that eat those plankton, so reducing the number of fish that Grebes can predate upon. In other cases, invasive salmonids cause population declines less directly, such as Grebe numbers being reduced by bycatch in nets placed by fishers to catch salmonid fish. Studies of dietary overlap between invasive species and native grebe species has helped wildlife managers and conservationists to protect other species of grebe, such as work on the overlap in the diet between the Hooded Grebe *Podiceps gallardoi* and invasive Rainbow Trout *Oncorhynchus mykiss* in Patagonia (Lancelotti *et al.* 2015). Understanding the diet of the Titicaca Grebe, and how it varies across age classes, can help to indicate by which mechanisms the introduced salmonids influence the Grebe's population, and whether a particular life stage is most affected. Usually, the intersection between demography and human–wildlife conflict focuses on the demographics of the species that problem species target and human values, such as livestock (i.e. De Azevedo & Murray 2007), though in some cases they have focused on the demographic differences in individuals causing said conflict (Mattisson *et al.* 2014). The latter can help target interventions on the particular individuals that are most likely to cause issues in 'problem' species, while the former can help target which individuals need greater preventive measures to be protected. Given that we know that Grebe diet is extremely variable (Fjeldså 1981), we felt that it would benefit not just the understanding of the Grebe's ecology, but also its conservation, to explore at least one source of this variation, and age is one that is readily identifiable, making it theoretically easier to be the subject of education campaigns than more cryptic traits in this species, such as sex.

The Titicaca Grebe is piscivorous, and in the context of Lake Titicaca can be considered an apex predator (Servant-Vildary *et al.* 1992). The one study performed on the diet of this species was an analysis of 12 adult Grebes, caught in Laguna Umayo and near Piata, in the region of Huancané, over 40 years ago (Fjeldså 1981). This found that 94.4% of the diet by weight was *Orestias*, with the remainder being invertebrates, mainly aquatic insects of the genus *Buenoa* and the family Corixidae (Fjeldså 1981). This study also noted that there was significant variation in the diets of individual Grebes, but no attempt was made to determine the cause of this variability.

The objective of this study is to determine the extent of overlap between the target species of fishers and Grebes. As an ancillary to this main objective, we also have the mini-objective of determining if there is any age difference in the overlap between the target species of the Grebe and fishers. Knowledge of the actual dietary overlap between predatory species and species valued by humans is a first step in addressing actual or perceived human–wildlife conflict (Treves *et al.* 2013, Guerra 2019). Knowledge of any age-based variation in this overlap is important in understanding whether conservation efforts should be targeted at specific groupings within a species that causes problems for humans (Mattisson *et al.* 2014).

METHODS

Study sites and site description

Lake Titicaca is the world's highest altitude navigable lake and is shared between Peru and Bolivia (Wirrmann 1992). Lake Titicaca is a freshwater ichthyological diversity hotspot, with over 90% of species being endemic (Albert *et al.* 2011). All save two native species of Lake Titicaca are members of the genus *Orestias*, and the other two are pencil catfish of the genus *Trichomycterus* (Vila *et al.* 2007). Although little is known about the ecology of the fishes of Lake Titicaca before the introduction of invasive species in the 20th century, today, most native species are relatively slow and primarily reside near the shore, particularly in areas with high levels of vegetation (Lauzanne *et al.* 1992, Vila *et al.* 2007). In the 20th century, invasive predatory fish species were introduced, such as Rainbow Trout and Pejerrey, to Lake Titicaca (Everett 1973, Laba 1979, Orlove 2002). These tend to be faster than native species and are found in open water as well as near the shore (Lauzanne *et al.* 1992, Vila *et al.* 2007).

Although the Titicaca Grebe is thought to have experienced significant population decline over the last 50 years, this itself represents a decline from earlier times. Nineteenth century descriptions of Lake Titicaca state that the Titicaca Grebe was one of the most common, or the most common, bird species on the lake (Sclater & Salvin 1869, Squier 1877). This significant population decline is associated with increased fisheries bycatch, which has followed increased fishing intensity in Lake Titicaca over the 20th century (Martinez *et al.* 2006). Fisheries have existed in Lake Titicaca for thousands of years (Capriles *et al.* 2014), but expanded significantly in the mid-20th century with the above-mentioned fish introductions (Everett 1973, Laba 1979, Orlove 2002). These introductions were followed by significant declines of Grebes, as well as of other endemic Lake Titicaca species, such as the Titicaca Giant Frog *Telmatobius culeus* (Angulo 2008), and has been linked with the probable extinction of the Titicaca Orestias *Orestias cuvieri*, an endemic pupfish (Hall & Mills 2000, Vila *et al.* 2007). The capture of Grebes

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as a fishery bycatch has also increased hostility towards it from local fishers, who blame Grebes for competing with them for limited fish stocks and for breaking nets (Quispe *et al.* 2023, Villar *et al.* 2024a).

Samples were collected on the Peruvian side of Lake Titicaca. We distinguish between three areas on the Peruvian side from which we collected samples: Huancané, Huata and Chucuito (Fig. 1). Huancané is on the north side of Lake Titicaca, with little aquatic vegetation and deep water. Huata is on the north side of Puno Bay, and on the edge of a large expanse of thick totorales, or swamp of *Schoenoplectus californicus* subsp. *tatora*, and probably other sub-species or species of the same genus (Paola Velásquez-Noriega, pers. comm.). Chucuito is on the south side of Lake Titicaca, in an area with little aquatic vegetation but shallow waters. These areas are highlighted on the maps in Figure 1.

Fishers' target species

Fishers' target species were gleaned from semi-structured interviews as part of a larger ethnobiological study of fishers in Lake Titicaca that took place in 2022. As part of this larger study, fishers were asked to provide their opinion of the species on a Likert Scale, with 0 being the most negative and 10 the most positive, and then were asked to justify their opinions of the Grebe. For full results and methodologies, see Villar *et al.* (2024a). Fishers were also asked which fish they targeted and were permitted to list multiple species. This free-listing technique is well established in ethnobiology for studying the extent of use of species and the importance of different species to a society (Balée 2013, Silva *et al.* 2019), including for studying the target species of artisanal fisheries (Messias *et al.* 2019, Braga *et al.* 2020). We then calculated the percentage of fishers that targeted each species, to determine what percentage of fishers target the same species as the Grebe. Fishers who said they fished indiscriminately were listed as fishing all species in Lake Titicaca. Furthermore, we surveyed the largest fish market in the Peruvian Altiplano, that of Unión y Dignidad in Puno, to provide an independent control for the target fish species of the fishing industry in Lake Titicaca, although this was not included in the dietary overlap analysis between fishers and Grebes. This survey of the fish market was to validate that the fish species that fishers said that they were targeting were indeed the species being targeted.

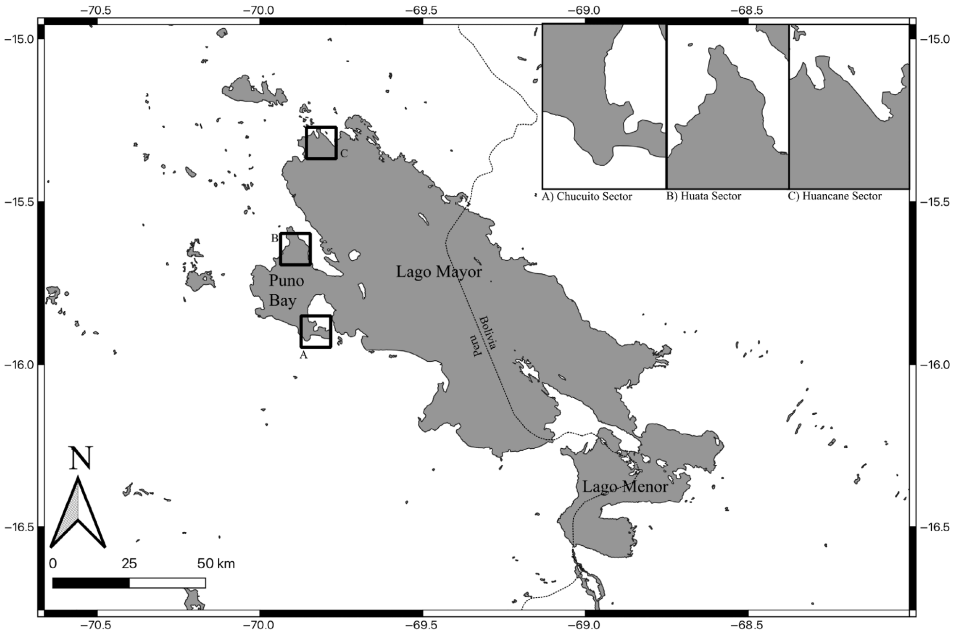


Figure 1. Map of Lake Titicaca, with the Huata, Chucuito and Huancané Sectors, where birds were collected, shown in insets.

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Fishers gave species names using the local taxonomy of fishes that exists in the Altiplano. Although variation exists between the most common folk taxonomy of the region, it places fish in one of six categories. These are: ispi – small native pupfish, primarily *Orestias ispi*; carachi – all pupfish larger than ispi; mauri – pencil catfish, primarily of the species *Trichomycterus rivulatus*; suche – catfish larger than the mauri; Pejerrey and trucha, or trout. Ispi, carachi, mauri and suche are all local vernacular names for these categories, and are shared between Quechua, Aymara and Spanish speakers. For the purposes of this study, we merged the categories of carachi and ispi into a category of *Orestias* sp.

Specimen collection, stomach content analysis and data sources

Our analysis is based on specimens caught as bycatch by fishers. The possible effects of bias caused by this sampling method are considered in the Discussion. We worked with fishers in the summer of 2008 to collect birds caught as bycatch in their nets. All individuals ($n = 45$) were preserved in 40% ethanol while being transported to the Universidad Nacional del Altiplano in Puno, Peru, for stomach-content analysis, which was undertaken on the same day as the collection of specimens. Individuals were identified as either adults or juveniles on the basis of plumage. Juveniles have lighter brown feathers on the upper body and white feathers on the belly, whereas adults have darker brown feathers on the upper body and a more rufous-coloured belly. This difference in plumage between adults and juveniles is characteristic of the species (Fjeldså 2004).

The oesophagus, proventriculus and gizzard were removed from each bird via an incision on its ventral side. We measured volume of the stomach content of each individual, and identified the contents of the stomach by reference to a voucher collection, identifying fish by otoliths. We counted both abundance and presence/absence of prey to the lowest possible taxonomic level, allowing for both 'presence–absence' and 'numerical' analyses (Hyslop 1980). The latter can include counting the number of individual prey items as well as the volume of prey, but following work on the unreliability of volume estimates from guts (Rindorf & Lewy 2004), we have counted the number of prey items for our numerical analysis. Numerical analysis tends to overestimate the importance of small prey due to reporting numerous prey that constitute an energetically insignificant percentage of the species' diet as more important than larger but less numerous species (Crisp *et al.* 1978, Ahlbeck *et al.* 2012), but allows an assessment of the relative importance of different prey species (Hynes 1950). Presence–absence methods tend to be more robust mathematically (Baker *et al.* 2014, Buckland *et al.* 2017), but can underestimate the importance of species in diet, especially for specialist species. Following the recommendation of a recent review on gut content analysis (Amundsen & Sánchez-Hernández 2019), we have combined these approaches to attempt a more complete understanding of the diet of the Titicaca Grebe. Because our interest was on conflict between the Grebe and the fishers, and due to difficulties in identifying semi-digested invertebrate remains, we focused on identifying the fish species in the stomachs of Grebes, and placed invertebrates into four categories: insects, amphipods, molluscs and miscellaneous invertebrates. Due to the local folk taxonomy of fisheries, and the limitations of identifying semi-digested fish remains, we did not identify pupfish to the level of species.

Quantitative analysis

Schoener's Diet Overlap Index (Schoener 1970) was used to measure the diet overlap between juvenile and adult Grebes across all sites, and between juvenile and adult Grebes within sites. Schoener's Overlap Index is calculated as $D = 1 - 0.5\left(\sum_{i-1}^{n} \left| p_{ij} - p_{ik} \right|\right)$, where p_{ij} is the proportion of prey type i in the diet of population j, and p_{ik} is the proportion of prey type i in the diet of population k. The Index, which ranges from 0 (no overlap) to 1 (complete overlap), is generally used to study niche overlap between species (e.g. Ogloff *et al.* 2019, Tesfaye *et al.* 2021), but has been used to study diet overlap of populations within species (e.g. Mabragaña & Giberto 2007, Šantić *et al.* 2012, Anastasopoulou *et al.* 2013). An Index value greater than 0.6 is of biological significance, suggesting that the two populations have the same dietary niche (Wallace 1981). In this instance, the Index measures the overlap in target species by the Grebe and the fishers. This was done both for numerical and for presence–absence counts of prey. In addition to diet overlap between adult and juvenile Grebes, we also used diet overlap between fishers and Grebe, using the response of the target fish species of the fishers as a proxy for fisheries dietary overlap. We did this solely for presence–absence counts, because, although fishers did tell us their average weekly catch, lack of knowledge of the Grebe's digestive system means that we were unsure of the timeframe of their diet that was represented in the stomach samples. For the purposes of the diet overlap analysis between fishers' self-reported catch and Grebe stomach contents, ispi and carachi were merged into one *Orestias* sp. category, and we merged mauri and suche into one *Trichomycterus* sp. category. We performed the analysis both with all prey categories and solely with fish, the latter allowing us to focus on the most likely area of direct competition between fishers and Grebes. We believe that it makes sense to compare all categories between fishers and Grebes even though fishers do not target invertebrates, and their nets do not catch invertebrates, as the goal of

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this study is to look at the overlap between the target species of fishers and Grebes. By definition, this has to involve looking at species that are non-target species for both parties. All quantitative analyses were conducted using R software version 4.3.1, and graphs were made using the ggplot2 library (Wickham 2016, R Core Team 2023).

RESULTS

We interviewed 221 people, of which 63 were fishers. Full detailed results, including the breakdown of the number of individuals interviewed per location, can be found in the supplemental material of Villar *et al.* (2024a). Fishers were not asked for how long they had been involved in fisheries. The most commonly targeted fish species was carachi (66.66% of fishers), followed by Pejerrey (57.14% of fishers), ispi (25.40% of fishers), mauri (20.63%), trout (17.46%) and suche (9.52%). The average score fishers gave to the Grebe was 4.82, suggesting overall slightly more negative opinions than positive ones. The cause of these negative views was that the Grebe is seen as competition for scarce fish resources, and that the Grebe breaks nets when it gets caught as bycatch. Twenty-seven fishers directly mentioned that they viewed the Grebe as competition for fish as a reason for their opinion. Of these, 18 made no species-level distinction of which fish the Titicaca Grebe ate, and five accused the Grebe of eating trout and Pejerrey directly. Although it was not part of the planned semi-structured survey, all save two mentioned declines in fish abundance during their time as fishers. There are seven stands which primarily sell fish from Lake Titicaca in the Unión & Dignidad fish market in Puno. Which fish they sell varies on availability each day, given that most fishmongers are women who get fish from their husbands or buy it from fishers coming to Puno in the early hours of the morning, save for one whose fish solely comes from her husband's fish farm. All, when asked, preferred to sell trout or Pejerrey, but all save the one who solely sold farmed trout sold native species as well. Trout fry were commonly found in the piles of ispi being sold in the fish market, suggesting that fishers are accidently catching many non-target fish in their smaller-mesh nets.

We examined the stomach contents of 45 Grebes, consisting of 19 juveniles and 26 adults. Fifteen Grebes were caught in each sector: in Chucuito, 5 were adults and 10 were juveniles; in Huata, 12 were adults and 3 were juveniles; and in Huancané, 9 were adults and 6 were juveniles. We found that there was no significant difference between the diets of juvenile and adult Grebes. We found no biologically significant dietary overlap between fishers and Grebes when taking non-fish prey items into account (Table 1). However, we found a biologically significant overlap between the target fish species of fishers and adult Grebes, and a near-significant overlap for fishers and juvenile Grebes and when considering all Grebes together. Dietary contributions of prey species for fishers and Grebes and for different age classes of Grebes are summarized in Figures 2 and 3, respectively. We found no evidence of the Grebe eating the fry of either of in the invasive fish species in Lake Titicaca.

Table 1. Schoener's Overlap Index indicating the dietary overlap between adult and juvenile Grebes, and between Grebes and fishers.

Populations being compared	Schoener's Overlap Index
Grebe juveniles and Grebe adults – numerical count, all prey types	**0.811**
Grebe juveniles and Grebe adults – presence–absence count	**0.899**
Fishers and Grebe adults – presence–absence count, all prey types	0.162
Fishers and Grebe juveniles – presence–absence count, all prey types	0.193
Fishers and all Grebes – presence–absence count, all prey types	0.172
Fishers and Grebe adults – presence–absence count, fish only	**0.602**
Fishers and Grebe juveniles – presence–absence count, fish only	0.558
Fishers and all Grebes – presence–absence count, fish only	0.588

Results showing a biologically significant dietary overlap (>0.6) are in bold.

DISCUSSION

We found that fishers have negative attitudes towards the Titicaca Grebe, which are caused by a variety of factors, including perceived overlap in the target species of the Grebe and the fishers. This negative perception of the Grebe is a significant barrier to conservation efforts towards the Grebe. However, previous studies have already highlighted this fisher–Grebe conflict, and its role in the conservation of the Titicaca Grebe (Quispe *et al.* 2023, Villar *et al.* 2024a). This study provides the first empirical test of this perceived overlap in target species of fishers and Grebes and provides the first empirical evidence for ameliorating this source of conflict.

We found mixed evidence for this common assertion among fishers that the Grebe is direct competition for fish species. The Grebe almost certainly targets members of the genus *Orestias* among its fish prey, and does not compete with the fishers for the more commercially lucrative trout or Pejerrey. This is also the case for

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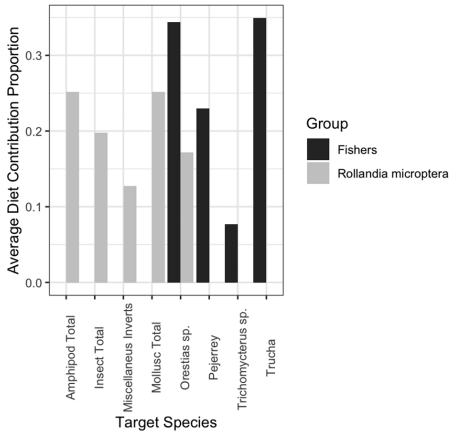


Figure 2. Comparison of average proportion contribution of each prey class to diet using numerical counts of prey items between fishers and Grebes.

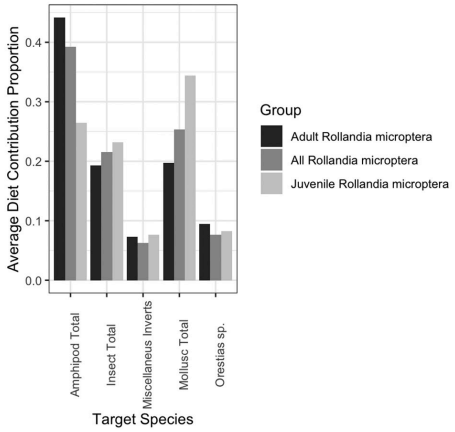


Figure 3. Comparison of average proportion contribution of prey items between Grebe age classes using presence–absence count results for prey items.

juveniles of the latter two, though it remains possible that some Pejerrey or trout fry are eaten by Grebes, given the inherent uncertainties present in identifying small partially digested fish remains (Buckland *et al.* 2017).

As a result of the conservation status of the Titicaca Grebe it would have been unethical to take birds specifically for diet analysis. Nevertheless, it is possible that sampling only from fishery bycatch could produce a bias, as being trapped in a net implies fishing for the same prey. Our analysis may, therefore, have overestimated the degree of diet overlap that exists between fishers and Grebes overall. However, we cannot dismiss the possibility that genuine competition exists between fishers and Grebes. Most fishers target at least some *Orestias* species, even if they indicated that they would rather be targeting rarer Pejerrey and trout.

These results lead us to suggest that there may exist genuine (as opposed to perceived or assumed) competition between fishers and Grebes for *Orestias*. Furthermore, we have to consider the 14-year time difference between the fishing interviews and the dietary analysis. It is possible that the competition could have changed as the result of changes in resource use by fishers or Grebes in that time, due to changing availability of fish in Lake Titicaca. However, if change has occurred, we suspect it would be towards more competition, and not less. We have no reason to believe that Grebes have begun to hunt trout or Pejerrey in the intervening years, but from the interviews with fishers we have reason to believe that there has been a move away from targeting trout and Pejerrey by human fishers, and towards targeting the more abundant, if less economically lucrative, native *Orestias* species.

The importance of *Orestias* indicates that the Grebe has not managed to change its diet following the introduction of salmonids and Pejerrey to Lake Titicaca, making the conservation of the endemic fish fauna crucial for the conservation of the Titicaca Grebe. The endemic fish fauna of Lake Titicaca has undergone significant declines due to invasive salmonids and pollution (Villwock 2001, Vila *et al.* 2007, Monroy *et al.* 2014), including the probable extinction of at least one species, the Titicaca Orestias (Hall & Mills 2000, Vila *et al.* 2007). If the Titicaca Grebe relies primarily on the native *Orestias* as its prey, and the populations of *Orestias* in Lake Titicaca have been reduced irrevocably by invasive species in the 20th century, it might be the case that the carrying capacity of Lake Titicaca for Titicaca Grebes is lower than it had been before these introductions. If this is the case, it might mean that the flocks of 300–400 birds described in the 19th century (Sclater & Salvin 1869) would not be sustainable today even if a fisheries moratorium to reduce bycatch were to be introduced and enforced.

Although the overlap in the 'diet' of the target fishes of Grebe and fishers was only biologically significant for adult Grebes, it was nearly so for juveniles and when considering all Grebes together. It is also interesting to note that juveniles consume many more molluscs compared with adults; in general, other grebe species prefer

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to eat amphipods to molluscs (Fjeldså 2004). This age difference in diet might indicate learning in this species, as adults learn to discriminate between amphipods and molluscs when hunting. However, overall, we found no difference between adult and juvenile Grebes, suggesting that they occupy the same dietary niche in Lake Titicaca.

Future research and conservation actions

Resolving human–wildlife conflict when the conflict is more imagined than real is already very difficult, as the attitudes of affected people can remain unchanged even after education (Treves *et al.* 2017). Resolving human–wildlife conflict when there are factual grounds for said conflict is even more difficult. We suggest that environmental education of fishers is required to teach how Grebes do not compete with them for most fish species in Lake Titicaca, especially not for the more lucrative trout and Pejerrey, though they do compete for the less lucrative native *Orestias*. The conflict occasioned by actual overlap between fishers and Grebes regarding *Orestias* cannot be resolved the way human–wildlife conflict has been dealt with in other contexts where predators hunt species on which humans rely, such as direct compensation schemes for individuals predated (Dickman *et al.* 2011, Ravenelle & Nyhus 2017), for practical reasons, though a compensation scheme for broken nets might be viable if done by the governments of either Peru or Bolivia. Instead, the Grebe must be turned from an economic problem species to one that provides economic value to the community (Woodroffe *et al.* 2005). There are several ways this could be done, including ecotourism (Gössling 1999), though it is likely that several potential models will have to be considered and tested before finding which one is correct for Lake Titicaca. These conservation strategies would have to be particularly mindful to take into consideration the rapid economic and social changes that the region around Lake Titicaca is undergoing, which have considerable impacts on people's uses and attitudes towards the natural environment of the lake (Villar *et al.* 2024b).

Further study of Grebe ecology and feeding habits could lead to more information regarding Grebe–fisher conflict, noting for example the potential for sampling bias through sampling bycatch, although ethical considerations must be in the foreground. Although this study focused on Grebe diet, studies of Grebe bycatch could reveal patterns of net types, net depths or geographical patterns in bycatch that could lead to conservation actions. Estimation of the total human fisheries catch in Lake Titicaca, and of the total Grebe fisheries catch, could help place the competition between fishers and Grebes for *Orestias* in perspective. Previous studies of Grebe diets in other study systems have found that predation by Grebes can be a greater pressure on fish populations than the total fisheries catch (Geiger 1957) or can be insignificant compared with human fishing activity (Markuze 1965), but it is difficult to predict a priori which it is in Lake Titicaca. Dietary isotope studies, which can help explain the finer variations in diet composition, especially when combined with gut contents analysis (Horswill *et al.* 2018), could also more precisely show which species of *Orestias* the Grebes and fishers compete for. The use of historical museum samples could inform on historical Grebe diets and be used to study the diet of life stages not included in this study, such as chicks. Zooarchaeological work on fish stable isotopes suggests that stable isotopes can distinguish between different *Orestias* species (Miller *et al.* 2010). We also recommend work on the effect of pisciculture on Grebe diet and bycatch, given the increasing number of fishers who are transitioning to pisciculture in Lake Titicaca (D. A. V., pers. obs.).

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AUTHOR CONTRIBUTIONS

D. A. Villar: Writing – original draft; writing – review and editing; formal analysis; software; data curation; conceptualization; validation. **Ever Yanes:** Investigation; writing – review and editing; validation; methodology; conceptualization; data curation. **Edwin R. Gutiérrez Tito:** Investigation; methodology; writing – review and editing; formal analysis; data curation. **Andrew G. Gosler:** Writing – review and editing; supervision; methodology.

ETHICAL NOTE

None.

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None.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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The data used in this chapter can be found in Appendix B

8

Discussion

Main Findings

Over the course of this thesis, the Titicaca Grebe has gone from one of the most enigmatic species of the Altiplano to one of the best studied species of the region. Indeed, it could now be argued that ornithological efforts should turn to focus on the now lesser studied, but far more numerous, aquatic species of the high Andes, such as the Andean Coot (*Fulica ardesiaca*) and the Andean Gull (*Chroicocephalus serranus*). Here I briefly summarise each of the data chapters of this thesis, and how they build on each other to develop a fuller understanding of the Lake Titicaca socio-ecological system, and the role of the Titicaca Grebe within it.

1) Chapter 2 used satellite imagery to study whether habitat loss was a major driver of population declines in the Titicaca Grebe. This was prudent since this chapter was written when travel to Peru and Bolivia remained uncertain, and because of the role of habitat loss in the declines of other species (Caro et al., 2022). It found that since breeding territory for the Titicaca Grebe had increased slightly since 2001, loss of breeding habitat was unlikely to be the major driver of population declines in the Titicaca Grebe.
2) Chapter 3 provides the first estimate of the Titicaca Grebe population in twenty years. It offers an up-to-date number for conservationists and wildlife managers in the Lake Titicaca region seeking to conserve the species. It suggests that the Titicaca Grebe population increased since the last census in early 2003, a finding consistent with the results of Chapter 2.
3) Chapter 4 focuses on the position of the Titicaca Grebe within Andean society. Conservation requires the buy-in from local people, and this chapter studied what people think of the Titicaca Grebe. It showed that the Titicaca Grebe doesn't inspire strong feelings from most residents of the Altiplano, with the exception of fishermen,

who view it as a threat to their livelihoods. This chapter alerted me to the Grebe-Fisher conflict, and to the rapid changes in Altiplano attitudes towards nature, which are the subject of the rest of the thesis.

4) Chapter 5 discusses changing use of the Titicaca Grebe's primary breeding habitat, the totora wetlands. I found that the traditional management system of the totora wetland has collapsed as market forces make the totora sedge less important for daily existence in the Altiplano. I also discuss some of the ecological consequences of this change in use, and what potential impacts it could have on the Titicaca Grebe. This chapter also highlights how once the material basis for TEK is eroded, so is TEK.

5) Chapter 6 is the first ever attempt to estimate total fisheries bycatch in Lake Titicaca. I show that distribution models can be deployed successfully to map the probability of a location being subject to artisanal fisheries. A "problem" identified in this chapter is a tendency for fishers to misreport bycatch to such an extent as to provide biologically implausible numbers. This suggests that monitoring is required for a more accurate assessment of fisheries bycatch in Lake Titicaca.

6) Chapter 7 focuses on one of the fishers' primary complaints about the Titicaca Grebe; that it competes with them for commercially important fish. Using dietary overlap analysis, we show that while an overlap does indeed exist between the diets of Titicaca Grebe and the species targeted by fishers, it is driven primarily by the grebe targeting less commercially important fish, such as the native *Orestias* sp.

The Titicaca Grebe as an Ethnoecological Case Study

The focus of this thesis is on one species, and unapologetically so. In focusing on one species, I hope I have achieved two things. Firstly, I hope to have increased the natural history knowledge of one unique tip in the tree of life. Natural history, meaning the simple observation of nature without a firm hypothesis, is the basis of all other biology (Barrows et al. 2016), but has fallen into abeyance (Able, 2016). Secondly, I hope to have shown that even species which do not appear to have a significant cultural meaning still have a place in the human cultures which surround them, and understanding that place is crucial to that species' conservation.

The Titicaca Grebe is subject to many of the threats to biodiversity in the 21st century: invasive species, pollution, overexploitation, and climate change. Yet at the same time, it appears not to face several of the major threats to biodiversity that plague many other species, such as habitat loss. It also appears to have rebounded in population relatively quickly, suggesting either a remarkable ability to adapt to changed conditions, or the removal of whatever caused the significant population decline between the 1970s and the early 2000s. Like many species, amongst the harder to quantify threats it is facing is the loss of the biocultural background which traditionally surrounded it, and maintained the cultural landscape which it lived in. If I had included the Titicaca Grebe in a large meta-analysis of species at risk of extinction, of the sorts which are regularly published in high impact journals (i.e. Harfoot et al., 2021; Gumbs et al., 2024), it would likely have been coded as having fewer than 1000 individuals (IUCN, 2020). The Titicaca Grebe thus highlights that, for many poorly studied species, the figures collated in massive datasets on their conservation status or ecology could be misleading at worst, and outdated at best. This is not the first study to show the necessity of more detailed studies of

individual species for accurate conservation assessments (Haelewaters et al., 2024; Lees et al., 2020), but it does highlight how even in well studied clades, significant shortfalls can occur in our knowledge of conservation relevant information.

The Titicaca Grebe, and its ethno-ornithology, also serves as a case study of how ethnobiology, ethnoecology, and TEK, intersect with changing economic and cultural patterns in the 21st century. The Titicaca Grebe's place in Altiplano society, insomuch as it has a major one, is driven by its perception as a competitor and an irritant to fishers. Fishing in turn only became prominent in Lake Titicaca since the introduction of large, commercially valuable, species in the mid-20th century, suggesting that the Titicaca Grebe's position in Altiplano society would have been very different before c. 1950. At the same time, the Titicaca Grebe's breeding habitat, the totora wetlands, have seen an expansion even as their use has declined. That the Titicaca Grebe is not of significant cultural importance to the local indigenous people to Lake Titicaca, either in my research or in historical ethnographies of the indigenous peoples of Lake Titicaca (Forbes, 1870; La Barre, 1941; La Barre, 1946; La Barre, 1948; La Barre, 1951; Mishkin, 1946; Tschopik, 1946; Orlove, 2002), likely reflects that it is neither traditionally charismatic, like the culturally significant condor, or used for a practical purpose, like totora. The intersection between economics, TEK, ecology, and conservation remains understudied, but even in this one example, it's clear that one couldn't understand the changing extent of Titicaca Grebe breeding ground without understanding the economic, as well as cultural, context. Some ethnobiologists tend to assume antiquity in TEK, but the example of the Titicaca Grebe shows that TEK might be a lot less "T" than often supposed (Pierotti, 2010; Clarke, 2023) – the ethno-ornithology of the Titicaca Grebe shows how false this assumption can be, and should spur other ethnobiologists to study the drivers of change in TEK.

Future and Ongoing Research

Ongoing Research

While this thesis represents a significant step forward in the study of the Titicaca Grebe, much remains unknown about this species. Some information collected has been excluded from the thesis due to the limitations of space and time. This includes information on the breeding biology, nest architecture, and territory formation of the Titicaca Grebe, which I had the pleasure to observe in Isla Suasi in 2023 and in Chucuito in 2024. These simple ethological observations exist purely as notes, but I hope to turn them into natural history notes in the near future. There is also work which was begun during this thesis, but remains unfinished. This includes studying the change in the diet of the Titicaca Grebe since the introduction of invasive species in the 20th century. Historic samples of grebes and fish have been the subject of stable isotope analysis, but delays by the relevant authorities in Peru and Bolivia have meant that contemporary samples have not been analysed yet. However, they are to be analysed in the coming months, meaning that this aspect of the Grebe's biology should shortly become well known.

Future Research Directions

Areas of Titicaca Grebe biology not covered by this thesis

Even well studied species and locations continue to provide biologists with interesting questions (Kohler, 1994; Perrins & Gosler, 2011). Thus, we can only provide some of the broader aspects of the biology of the Titicaca Grebe which were not touched on during this thesis, and

some of the research questions which have been opened by this thesis, but which weren't answered by it.

Three major aspects of the Titicaca Grebe's Biology were not addressed during this thesis, and should be studied for a complete monograph: its physiology, its genetics, and its movement ecology. Other high-altitude birds, including those native to Lake Titicaca, have physiological adaptions which permit them to live in this harsh environment (McCracken et al., 2009; Díaz et al., 2024). It is very likely that the Titicaca Grebe has similar physiological adaptions. I have been contacted by a doctoral candidate at the University of Miami interested in studying the physiology of the Titicaca Grebe. She is part of a lab which studies the physiology of high-altitude birds, including several studies on the physiology of Anatids in Lake Titicaca (McCracken et al., 2009; Ivy et al., 2019; McCracken et al., 2024; Díaz et al., 2024).

The Titicaca Grebe genome has never been sampled. The most recent molecular phylogeny of Podicipedidae excluded genetic information of the Titicaca Grebe (Ogawa et al., 2015). Furthermore, nothing is known about the population genetics of the Titicaca Grebe. Given the evidence of a rapid population decline followed by a relatively rapid recovery, there is a strong change that the Titicaca Grebe suffers from a lower effective population size due to the bottleneck it went through, which could harm more long-term conservation efforts (Frankham, 2005). However, it is possible that this bottleneck might not be as deleterious as it would be for most species, given the evidence that some species which have evolved over long periods in small areas, such as islands, undergo strong purging selection against deleterious alleles (i.e. Robinson et al., 2018). This pattern however is far from universal (i.e. Kennedy et al., 2014), and only genetic analysis of present and historic Titicaca Grebe samples could answer whether

the bottleneck has reduced the effective population size of this species to a degree that should worry conservationists.

Knowledge of the Movement Ecology of the Titicaca Grebe would answer several outstanding questions of this species, such as whether pairs show fidelity to the same nest site year after year, whether there are seasonal movements of grebes between the wet and the dry season, and whether feeding territories are partitioned akin to how breeding territory is partitioned. Knowledge of the depth to which Grebes dive would also be useful in any anti-bycatch conservation measures which might be enacted in the future. The movement ecology of the Titicaca Grebe was originally proposed to be studied in this thesis, and plans had been made for the attachment of Time-Depth Recorders and GPS. I am aware that there is currently a project which has been approved by the Universidad Nacional del Altiplano on the movement ecology of the Titicaca Grebe which may shed light on these questions.

Questions about Titicaca Grebe biology and Lake Titicaca Social-Ecology raised by this Thesis

Chapter 3 is the first population census of the Titicaca Grebe, but it is only a snapshot. Without constant, or at least regular, monitoring of the population numbers, there is a risk that this thesis will become another dated data point used by managers in future years. It is unclear whether the Titicaca Grebe population fluctuates significantly year by year, or what might drive population changes. We know that the Titicaca Grebe can quickly colonise flooded areas in particularly wet years (Konter, 2006), but we do not know how drastically its population declines in dry years. This latter point is particularly important given both the recent severe drought in the Altiplano (Gutierrez-Villarreal et al., 2024), and that most climate change models suggest that the Central Andes will get drier over the coming century (Zazulie et al.,

2017; Pabón-Caicedo et al., 2020). Ideally, these surveys could be done using mark-recapture or bird ringing studies, which are much more accurate than SDMs in estimating population sizes (Iijima, 2020). However, given that there is no licensed bird ringer in the entire Puno Province, this seems like an unlikely prospect.

Chapter 6 attempted to solve a long-standing problem for conservationists in Lake Titicaca, using an innovative combination of LEK and distribution modelling to address the lack of reliable information on bycatch numbers. It proved to be a partial success; the distribution modelling was shown to be useful in studying the spatial distribution of artisanal fisheries. However, the responses of fishers suggest that self-reporting from memory cannot be used as a reliable indicator of the extent of fisheries bycatch in Lake Titicaca. Accuracy could be improved by fishers carrying logbooks with them as they fish, but ultimately a formal monitoring programme is required to know the extent of both fisheries catch and bycatch in Lake Titicaca.

I touched upon pisciculture in this thesis, but didn't focus on it as much as I did on fisheries. This was because the literature which existed when I was preparing my interviews only mentioned pisciculture as a minor industry. Research in other regions has shown that pisciculture can have contradictory effects on waterfowl populations. In some cases, pisciculture becomes a supplementary food source for birds, becoming a boon to their conservation (Burr et al., 2020a; Cheng et al., 2022). However, the habit of piscivorous birds eating farmed fish can make them targets for persecution (Burr et al., 2020b; Sun et al., 2020). Pisciculture can also pollute the regions where it occurs (Navedo et al., 2021; Skirtun et al., 2022), and the fish meal used to feed commercially important carnivorous fish, such as salmonids, can reduce the amount of available wild fish for piscivorous birds to feed on (Troell et al., 2014). Given the

density of Titicaca Grebes around fish farms, I am tempted to speculate whether it has been a net benefit to this species, but more research is needed to tell whether this is the case.

A repeated finding of this thesis is that TEK requires a material basis to continue to exist. This would seem to support the "Trial-and-error" hypothesis for its transmission, which suggests that TEK co-evolves with a landscape (Pierrotti, 2010; Menzies, 2006). This would also suggest that TEK changes both due to environmental changes, and to changes in how cultures interact with their environment. There is evidence from other regions that species extirpation, extinction, and environmental degradation are linked with the erosion of TEK (Gómez-Baggethun et al., 2013; Tuvey et al., 2018), but there is as of yet no systematic study of the change of TEK over long time periods, and the drivers of this change. This could be studied using cultural evolutionary and ethnohistorical methodologies (Albuquerque et al., 2015). Given the Andes' almost unique position of having several centuries of writing about traditional indigenous practices, including what we would now term TEK (Murra, 1970; Gade, 1999; Bussmann et al., 2006), it would provide a perfect region for such a case study. More short-term studies on this theme could be undertaken around Lake Titicaca, focusing, for example, on the effect of tourism, especially amongst the Uru, in changing TEK.

Epilogue

The Titicaca Grebe remains a poorly studied endangered species. More work is needed to conserve it, and ensure that it is around to be enjoyed and studied by ornithologists and the people of Lake Titicaca for generations to come. That said, after this thesis, a lot more is known about this species than was known beforehand. There is now information on its

population size, its diet, its place in Andean society, and the distribution of its greatest threat, fisheries bycatch. Up until now, this species remained an enigma, and its conservation based on hunches rather than science. This DPhil provides a basis of information for this species for future conservationists, ornithologists, and ethnobiologists. It also provides a framework for others interested in studying ecology and ethnobiology through the lens of a single non-charismatic species, something which I can only hope will occur with more frequency.

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Appendix A: Interview Questionnaire

Consent:

Le haré algunas preguntas sobre el uso de los recursos naturales, la naturaleza y su demografía, como parte de mi tesis doctoral de la Universidad de Oxford. Es totalmente voluntario para usted proporcionar esta información y puede negarse a proporcionar cualquier dato que desee. También puedes abandonar la entrevista en cualquier momento. Es completamente anónimo y no habrá forma de identificarlo. ¿Estás de acuerdo en que te haga algunas preguntas?

Sección Demográfica:

¿Cuántos años tienes?

¿Cuál es su religión?

¿Dónde nasciste?

¿Cuál es su comunidad?

¿Cuál es su nivel de educación máxima?

¿Cuál es su trabajo?

¿Tiene un trabajo secundario? (Solo si dicen sí) ¿Cuál es?

¿Qué lengua usted habla en casa?

¿Cuántos idiomas habla? ¿Cuáles? ¿Qué lengua usas en casa?

¿De cuántas personas está conformada su familia?

Sección de Conocimiento y Actitudes:

¿Conoce el zambullidor del Titicaca?

¿Conoce esta ave? (mostrar foto)

¿Cómo se llama esta ave? (de la foto)

Siendo 1 muy mala opinión del zambullidor del Titicaca, y 10 es muy buena opinión, ¿Qué piensas del zambullidor?

¿Por qué tiene esta opinión del zambullidor?

Siendo 1 que no sabe nada del zambullidor de Titicaca, y 10 que sabe mucho del zambullidor, ¿Qué sabes del zambullidor?

¿Qué podría decirnos del zambullidor?

¿Cómo utiliza al zambullidor? Por ejemplo, uso alimentario, ornamental, medicinal, mascota, comercial, mitos o leyendas, indicador ambiental, cinegético, etc.

¿Estaría usted dispuesto a realizar actividades para apoyar a la conservación del zambullidor del Titicaca?

¿Sabía usted que el zambullidor del Titicaca es una especie en peligro de extinción? (Se pregunta esta pregunta, y las próximas dos también, solo al final, como preguntas penúltimas)

¿Sabía usted que este zambullidor solo vive en el entorno del lago Titicaca?

Sabiendo que el zambullidor está en peligro de extinción y solo vive en el entorno del lago de Titicaca, ¿estaría usted más dispuesto a realizar actividades para apoyar a la conservación del zambullidor del Titicaca?

Preguntas para Pescadores:

¿Con qué frecuencias capturas aves en sus redes?

¿Has capturado un zambullidor en los últimos seis meses?

no

¿Qué haces con las aves que se quedan en sus redes? ¿Es diferente con el zambullidor que con otras especies?

¿Qué tipo de peces prefieren pescar?

¿Qué tipo de red usas?

¿Cuántas redes tienes, y de qué tamaño?

¿Cuánto tiempo dejas las redes en el agua?

¿Dónde pones las redes cuando estás pescando?

Comparación Con Otras Aves en el Lago Titicaca y Otras Preguntas Etnobiológicos:

¿Utiliza como medicina algún animal del lago Titicaca? ¿Cuáles usos tienes?

¿Hay algún ave que le gustaría que abunde más en el lago Titicaca?

¿Por qué elegiste esa ave?

Conclusión:

¿Le gustaría hacer un comentario adicional?

Appendix B: Data Availability

Data used to support this thesis can be found through the following link:

https://osf.io/gt7fj/?view_only=ff2a32f41faf4edeabde07331e11cdd7