Bird Conservation International

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Research Article

Cite this article: Marshall HH, Moloney CL, Glass T, Grundy R, Schofield A, Ryan PG (2025). The spread and status of the Gough Moorhen *Gallinula comeri* on Tristan da Cunha. *Bird Conservation International*, **35**, e20, 1–7 https://doi.org/10.1017/S0959270925100099

Received: 28 August 2024 Revised: 05 March 2025 Accepted: 23 April 2025

Keywords:

Gallinula comeri; Oceanic Islands; Population size; Rallidae; Range spread

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The spread and status of the Gough Moorhen Gallinula comeri on Tristan da Cunha

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Summary

Rallidae are frequent colonists of oceanic islands and are often susceptible to introduced predators. The Tristan Moorhen *Gallinula nesiotis* was endemic to Tristan da Cunha, South Atlantic and is thought to have gone extinct in the late nineteenth century. The closely related Gough Moorhen *G. comeri* was introduced to Tristan da Cunha from neighbouring Gough Island in 1956. We report historical records of their spread across Tristan da Cunha and the results of a population survey undertaken in February–March 2024. Gough Moorhens are now found across the entire island wherever there is suitable habitat from sea level to above 900 m elevation. Gough Moorhens prefer fern bush habitat on the Base, the plateau above the steep coastal cliffs. The total population is approximately 41,500 birds (95% confidence interval 24,000–72,000). Our density estimates (3–6 birds/ha) are similar to estimates for Gough Moorhens on Gough Island before the post-2021 population decline and are at the higher end of densities reported for oceanic island rallids, suggesting that the Tristan da Cunha population may be near carrying capacity.

Introduction

Birds of the family Rallidae (rails, crakes, and their allies) are frequent colonists of oceanic islands where they often lose the ability to fly to reduce their energetic demands (Gaspar et al. 2020; McNab 1994; Slikas et al. 2002). Convergent phenotypic evolution among island rallids creates taxonomic challenges, which have only recently been resolved with the aid of molecular-based phylogenies (e.g. Kirchman 2012; Stervander et al. 2019). The evolution of flightlessness is often rapid (van de Crommenacker et al. 2019) and is associated with high levels of extinction (Hume and Martill 2019), especially because flightless rails on oceanic islands are particularly susceptible to the introduction of non-native predators (Lévêque et al. 2021). An estimated 200-2,000 rallid species went extinct as people colonised oceanic islands across the Pacific Ocean (Curnutt and Pimm 2001; Steadman 1995), and the Rallidae remain one of the most threatened families of birds today (Lévêque et al. 2021). Conservation tools available to combat this threat include the eradication of non-native predators from islands (Jones et al. 2016; Spatz et al. 2022) and the translocation of populations (Miskelly and Powesland 2013; Spatz et al. 2023; Woinarski et al. 2016). Here, we report on the spread and population status of Gough Moorhens Gallinula comeri after their intentional translocation in the 1950s from Gough Island to Tristan da Cunha Island in the mid-South Atlantic.

Ancestors of Common Moorhens *G. chloropus* colonised the volcanic islands of Tristan da Cunha and Gough Island, but seemingly not the other islands in the Tristan da Cunha archipelago. They became flightless on both islands, yet despite appearing very similar, they are regarded as distinct species given their independent evolutionary histories (Groenenberg et al. 2008). The Tristan Moorhen *G. nesiotis* went extinct sometime in the latter half of the nineteenth century, after Tristan da Cunha was colonised by people in 1810 and probably before the arrival of Black Rats *Rattus rattus* in 1882 (Bond et al. 2019). Predation by feral cats and hunting for food by islanders using dogs are thought to have accounted for its demise (Beintema 1972; Woolley 1997).

Gough Island has not been settled by people, but the island has supported a South African weather station since 1956. Prior to the attempt to eradicate introduced House Mice Mus musculus from Gough Island in 2021 (www.goughisland.com), Gough Moorhens were common throughout fern bush (see Methods for a description) and tussock grass habitats below around 450 m elevation at densities of approximately 2.3 pairs/ha (Ryan 2007; Watkins and Furness 1986). Rails are particularly susceptible non-target species during rodent eradication operations using rodenticide (e.g. Oppel et al. 2016) and the vast majority of moorhens were killed by

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primary or secondary poisoning during the Gough eradication attempt (a safeguard population was taken into captivity during the operation; RSPB, unpublished data). This left most of the surviving individuals of the species on Tristan da Cunha.

Towards the end of the 1955-1956 Gough Island Scientific Survey, several Gough Moorhens were captured at The Glen on Gough Island for transport to the UK (Holdgate et al. 1956; Watkins and Furness 1986). On 15 May 1956, seven of these moorhens were released "east of the Settlement" on Tristan da Cunha (Richardson 1984), ostensibly to fill the vacant niche created by the extinction of the Tristan Moorhen (Woolley 1997). The exact location is unclear, but probably was close to Pig Bite, some 2 km east of the settlement (Martin Holdgate, personal communication; Woolley 1997; see Figure 1). Other releases might have occurred in the 1950s and 1960s (Woolley 1997), but the volcanic eruption on Tristan in 1961 meant that relatively little survey work was carried out during the period (the entire human population was evacuated until 1963). In 1972 a population of moorhens was discovered between Morgie's Gulch and Big Gulch on the "Base", the plateau above the sea cliffs, about 5 km east of Pig Bite and surveys in 1973 and 1974 indicated that moorhens were confined to ~8.5 km² on the Base in this area (Richardson 1984). By 1993, Woolley (1997) indicated that moorhens were widely distributed in suitable habitat with an estimated population of 8,000–10,000 birds but did not explain the basis of this estimate. By the early 2000s they occurred almost all around the island Base, with a population crudely estimated at 2,000 pairs (Ryan 2007). Historically there was some debate about whether the original moorhen populations on Tristan da Cunha and Gough Islands were the same or different species (Rand 1955). Comparison of samples collected in the 1990s from both islands with DNA from a museum skin collected on Tristan da Cunha in 1864 suggests that (1) each island originally held a separate species, Tristan Moorhens G. nesiotis and Gough Moorhens G. comeri and, (2) the moorhens currently on Tristan da Cunha are Gough Moorhens, not Tristan Moorhens (Groenenberg et al. 2008).

The current population status of Gough Moorhens on Tristan da Cunha is uncertain and the need to resolve this has become particularly acute due to the recent severe decline of the population on Gough Island. This paper collates historical records of the spread of Gough Moorhens on Tristan da Cunha and estimates their population in 2024 based on a series of repeated counts around the island.

Methods

Study area

Tristan da Cunha (37.11S, 12.28W) is the largest island (96 km²) in the Tristan Archipelago. It is an active volcano, some 200,000 years old, that last erupted in 1961 (Hicks et al. 2012; Ryan 2007). Marine erosion has outpaced fluvial erosion, resulting in steep coastal cliffs around much of the island's coast. The few areas of more or less level ground near sea level, i.e. the Settlement Plain, the Caves, Stony Hill, and Sandy Point (Figure 1), have been largely cleared for agriculture and do not provide sufficient cover for moorhens. Inland of these areas, and along much of the coast, the steep cliffs rising 300–900 m above sea level are mostly covered in fern bush, the diverse plant community characterised by two large, distinctive species: Bogferns Lomariocycas palmiformis (until recently known as Blechnum palmiforme) and Island Trees Phylica arborea (Ryan 2007; Wace and Holdgate 1958). The coastal cliffs along the western side of the island from Big Green Hill to Gipsy's Gulch are

dominated by Bogferns, whereas those around the eastern side of the island typically have Island Tree woodland over a short fern understorey dominated by *Austroblechnum penna-marina* (until recently known as *Blechnum penna-marina*). Most of the Base, below around 900–950 m, also supports fern bush, with more exposed areas covered by Bogferns, which intergrade into *Phylica* woodland in more sheltered, lower-lying areas. At higher elevations the fern bush is replaced by montane grassland, dominated by the introduced grass *Holcus lanatus*, which is in turn replaced by alpine feldmark and scoria at around 1,300 m (Ryan 2007; Wace and Holdgate 1958).

Historical observations

In addition to the published observations on the range of moorhens on Tristan da Cunha in 1973–1974 (Richardson 1984) and 1993 (Woolley 1997), we summarise observations of moorhens from 1982 to 1985, made by RG during 58 walks that traversed at least some potential moorhen habitat, in 1989–1991 (four ascents on to the Base), and 1999–2001 (a further four ascents on to the Base) by PGR and CLM.

2024 count protocol

The current distribution and abundance of Gough Moorhens were estimated from transects conducted from 8 February to 15 March 2024. All moorhens heard or seen were recorded during fiveminute sampling periods. At most locations, the observer walked slowly for 100 m during the count, which is the protocol used to survey Gough Moorhens on Gough Island (RSPB Gough Monitoring Manual, unpublished). However, where counts were conducted at the foot of the coastal cliffs that could not be safely scaled, the observer remained in the same area throughout the five-minute observation period. The distance to each moorhen heard or seen was estimated using a Nikon laser rangefinder. As most birds were only heard, the distance was measured to the location from which the bird was estimated to be calling; precision of the rangefinder was to the nearest 0.1 m, but inferred distances to calling birds probably were only accurate to within 10-20 m. Birds seen were classed as either adults or juveniles; the latter remain readily distinguishable by their brown plumage and drab bare parts until at least April, so they were easily recognised during the survey period.

Transect locations were chosen randomly to cover as much of the suitable habitat on the island as logistically possible. Transects were placed roughly 400 m apart, so birds estimated to be greater than 200 m from the observer were not used in the analyses. At least two counts were conducted at each point. Ideally these were conducted on separate days, or at least several hours apart, but in some hard to access areas it was necessary to repeat counts at shorter intervals. The date, time, location, and elevation of each count were recorded on the Gaia GPS app (www.gaiagps.com) in an iPhone 12, and a photograph of the habitat logged. Environmental data recorded included wind speed (scored 1–4, lowest–highest), cloud cover (0–8), and precipitation (raining/not raining).

On Tristan da Cunha, Gough Moorhens are largely confined to fern bush vegetation, which offers sufficient cover to provide protection from Brown Skuas *Catharacta antarctica* (Ryan 2007). They occasionally venture out into adjacent pastures to forage (e.g. visiting chicken coops on the settlement plain) but soon retreat to the cover of nearby fern bush. Counts were conducted in two main habitats: the coastal cliffs and in fern bush on the island Base (Figure 1). We divided the former habitat into western and eastern sections

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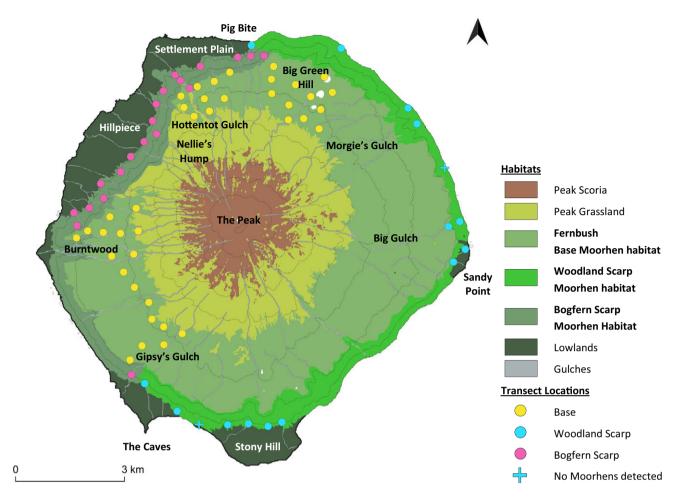


Figure 1. The distribution of transects conducted for Gough Moorhens in February–March 2024 in relation to the major habitat types on Tristan da Cunha (moorhen habitats shown in bold in the legend). Habitat types are based on the JNCC/SAERI habitat classification map for Tristan da Cunha (Environment Systems 2019); see text for details. Contour lines shown in 250 m intervals.

(hereafter "Bogfern scarp" and "woodland scarp"; Figure 1), because the short fern understorey in the woodlands along the eastern cliffs provides less cover for moorhens. It would be ideal to also split the Base transects into Bogfern and woodland, but the two intergrade, and few transects were conducted in dense woodland habitat because of the difficulty of access to this habitat. Counts were also conducted at 12 transects in the montane grassland on the lower slopes of the central peak, and one on top of the Hillpiece, a pasture-covered hill on the coastal plain, but these were not included in the analyses as no moorhens were recorded in these habitats. Access to the coastal cliffs was limited to a few paths (e.g. Big Green Hill, Hottentot Gulch, Burntwood, and Gipsy's Gulch), so additional transects were conducted along the base of the cliffs, typically where pastures gave way to fern bush vegetation.

Data analysis

We estimated the abundance of moorhens at 81 transects, each with two repeat counts, using binomial mixture models (Royle and Nichols 2003; Royle et al. 2005). These models produce an overall estimate of abundance in the areas surveyed by linking estimates of individual abundance and detection probability in a hierarchical fashion. Specifically, we used the mixture models developed by Royle (2004) for spatially replicated counts.

We included time of day, wind speed, and cloud cover as predictors of detection probability in our models based on personal observation that these were likely to affect detection and previous studies using similar repeated transect survey design (e.g. Jones et al. 2020; Oppel et al. 2024). Time of day was fitted as a quadratic function to allow detection probability to vary non-linearly across the day. We did not include rainfall as only 5 out 162 counts were conducted whilst it was raining, and this was correlated with cloud cover – scored at 8 for all five of these counts. We expected moorhen abundance to be influenced by elevation and habitat type (Base, woodland scarp, and Bogfern scarp), however, by definition, these are associated as the scarp occurs at lower elevations below the Base. Therefore, we fitted separate models with elevation and habitat type predicting abundance and also fitted a model including a quadratic elevation term to test for greater moorhen densities at intermediate or extreme elevations. We then used Akaike's information criterion (AIC) to select the most parsimonious model, also comparing it with a null model with no predictors of abundance. We fitted all models using the "pcount" function in the unmarked package (Fiske and Chandler 2011; Kellner et al. 2023) in R (R Core Team 2023) and used a negative binomial abundance distribution as other distributions (e.g. Poisson) produced models that were poorly fitted and overdispersed. We set the maximum possible population size at each count (K) to 30 to ensure this did not restrict our model's abundance estimates (maximum number of birds detected in a

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single transect = 10; see Royle 2004). We used the "Nmix.gof.test" function in the AICcmodavg package (Mazerolle 2023) to assess each model's χ^2 goodness-of-fit and overdispersion parameter (ĉ). All continuous variables were scaled (mean-centred and divided by their standard deviation) to aid with model convergence.

Our models produced estimates of moorhen density within each transect area. To convert these into an overall estimate of population size for the model including habitat type as a predictor we extrapolated across the total area of the Base and scarp habitats. We extracted these areas from the JNCC/SAERI habitat classification map for Tristan da Cunha (Environment Systems 2019). We groundtruthed this map with vegetation and habitat observations recorded at each transect and included all areas classed as "light", "dark", and "shadow" vegetation as scarp moorhen habitat (i.e. areas on steep slopes where the lighting in the satellite imagery did not allow specific habitat classification but which our surveys on the ground showed were suitable habitat), and all areas classed as "Phylica bush" and "Blechnum palmiforme" as Base moorhen habitat (note, the taxonomy of Blechnum palmiforme was recently revised to Lomariocycas palmiformis but the classification used in this habitat map was created before this change). The estimated total moorhen habitat area was 5,525 ha: 3,935 ha on the Base, 921 ha of woodland scarp, and 669 ha of Bogfern scarp. To produce population estimates from models including elevation as a predictor, we divided this moorhen habitat area into 100-m elevation bands using the NASA Shuttle Radar Topography Mission data (NASA JPL 2013). We then used our elevation models to predict moorhen density for the elevation in the middle of each band (i.e. 50 m for the 0-100 m band) and extrapolated across the total area in each band to produce a population estimate.

Results

Historical spread

Following their discovery in 1972 at Longwood, surveys in 1973 and 1974 indicated that moorhens were confined to ~8.5 km² on the Base (Richardson 1984), which is roughly the area of suitable habitat between Morgie's Gulch and Big Gulch (Figure 2). By 1985, moorhens had expanded north-west to Big Green Hill and south all the way to Gipsy's Gulch in the south-west of the island (Figure 2). By 1989 they had extended west from Big Green Hill to the top of Hottentot Gulch, but only one bird was heard west of this gulch. In 1999, they were found on the lower slopes of Nellie's Hump but remained absent from there to Gipsy's Gulch (Figure 2). By 2024, they occurred all around the island and were recorded at all transects conducted between Nellie's Hump and Gipsy's Gulch (Figures 1 and 2).

2024 survey

Moorhen counts were repeated at 81 transects in suitable moorhen habitat on Tristan da Cunha. Access constraints resulted in most counts being conducted in the north-western half of the island between Gipsy's Gulch and Morgie's Gulch, but counts were conducted around most of the island's circumference (Figure 1). The total number of transects was 197, with most surveyed two (69%) or three (25%) times (range = 2–8). In total, 526 moorhens were estimated to be within 200 m of transect locations, most of which (97%) were first detected by their calls; only 16 birds were seen before they were heard. Most encounters were recorded as single birds, but 17 groups of two birds were counted. Of the 35 birds seen, only three were juveniles. Moorhens were recorded during 89.3% of

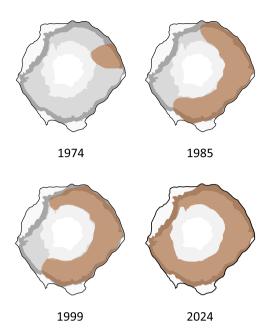


Figure 2. The approximate range of Gough Moorhens (brown) on Tristan da Cunha from 1974 to 2024.

transects, and on at least one occasion at all but two sites (97.5% of sites). Within each site, the mean number of moorhens recorded in each transect ranged from 0 to 7.5 (mean = 2.7 birds per count) and the coefficient of variation ranged from 0 to 1.7 (mean = 0.62).

The most parsimonious model of moorhen abundance contained the quadratic elevation term as a predictor of abundance (Tables 1 and 2). This model predicted that moorhen density was highest at elevations around 600 m (Figure 3). Using the moorhen densities predicted for each 100-m elevation band containing suitable moorhen habitat, this model estimated an overall population of 41,499 (23,952–71,918) Gough Moorhens on Tristan da Cunha (see Supplementary material Table S1). Although less parsimonious, the model estimating abundance by habitat type is also of interest. This estimated densities on the Base as 6.4 (3.1–13.2) birds/ha, in Bogfern scarp as 4.2 (1.9–9.1) birds/ha, and in woodland scarp as 2.9 (1.3–6.3) birds/ha. This produced an overall population estimate of 30,729 (14,788–63,875) birds. In all models the χ^2 goodness-of-fit P value was \geq 0.2, indicating a good fit, and \hat{c} ranged from 0.95 to 1.19.

Discussion

The Gough Moorhen population on Tristan da Cunha has spread from a small area on the Base east of Edinburgh of the Seven Seas

Table 1. Performance of models estimating the abundance of Gough Moorhens on Tristan da Cunha. See Nagelkerke (2004) for details of Nagelkerke's r^2 value. AIC = Akaike's information criterion

Predictors of moorhen abundance	AIC	ΔΑΙC	Akaike's model weight	Nagelkerke's r ²
Elevation + elevation ²	585.8	0.0	1.00	0.42
Habitat type	607.7	21.9	1.8×10^{-5}	0.24
Elevation	612.2	26.4	1.9×10^{-6}	0.18
None (null model)	625.9	40.1	2.0×10^{-9}	0.00

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Table 2. Best performing models estimating the abundance of Gough Moorhens on Tristan da Cunha. AIC = Akaike's information criterion

		Abundance	Detection probability	
Model	Variable	Parameter estimate (± SE)	Variable	Parameter estimate (± SE)
Elevation ² (AIC = 585.8)	Intercept	2.90 (± 0.28)	Intercept	-1.26 (± 0.36)
	Elevation	0.20 (± 0.07)	Time of day	-0.04 (± 0.07)
	Elevation ²	-0.47 (± 0.09)	Time of day ²	-0.09 (± 0.06)
			Wind speed ^b	0.05 (± 0.07)
			Cloud cover ^b	0.11 (± 0.07)
Habitat type (AIC = 607.7)	Intercept ^a	2.56 (± 0.37)	Intercept	-1.03 (± 0.50)
	Bogfern Scarp	-0.79 (± 0.18)	Time of day	-0.02 (± 0.08)
	woodland scarp	-0.42 (± 0.16)	Time of day ²	-0.09 (± 0.07)
			Wind speed ^b	0.01 (± 0.07)
			Cloud cover ^b	0.07 (0.08)

^aReference category = Base habitat.

Note: Parameter estimates are on the log and logit scale for abundance and detection, respectively. All continuous variables were scaled (mean-centred and divided by their standard deviation) to aid model convergence. Means (and standard deviations) in the raw data were as follows: elevation = 516.6 (302.9) m; time of day = 727.4 (130.4) minutes since midnight; wind speed score = 2.12 (0.67); cloud cover score = 5.44 (2.53).

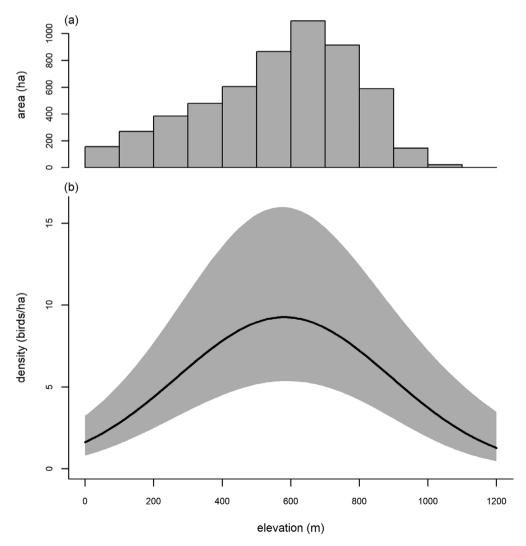


Figure 3. (a) The area of suitable moorhen habitat on Tristan da Cunha at 100 m elevation intervals from 0 to 1,200 m; there is no suitable habitat above this altitude (see Table S1). (b) Gough Moorhen density as a function of elevation predicted by the most parsimonious elevation model. The grey area shows the 95% confidence interval of the model prediction.

^bWind speed scored 1–4 (low-high), cloud cover scored 0–8 (low-high).

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(the only human settlement on the island; Settlement Plain in Figure 1), to now, in 2024, apparently occupying most, if not all, suitable habitat below around 900 m. We estimate its current population at 30,000–40,000 individuals.

After the initial introduction of seven birds in 1956 (Richardson 1984) and possibly some further releases in the 1960s (Wooley 1997), moorhens were not seen again until 1972, when they occupied ~8.5 km² on the Base between Morgie's Gulch and Big Gulch (Richardson 1984). Over the next decade, their range expanded rapidly to the south, but they only reached Big Green Hill in the north (Figure 2). At this time they were treated as pests (because they ate some albatross eggs) and were hunted by dogs when islanders worked with sheep on the Base, which was mainly in the area between the Ponds (unshaded circular areas just to the east of Big Green Hill in Figure 1) and Gipsy's Gulch. By 1999, the range had extended west from Big Green Hill across Hottentot Gulch, but moorhens remained absent from much of the western Base and adjacent coastal scarp. However, by the time of our survey in 2024, they had occupied all suitable habitat in this area (Figure 2).

Why have Gough Moorhens been so successful on Tristan da Cunha, when the seemingly very similar native flightless Tristan Moorhen went extinct in or around 1882, within 70 years of human colonisation (Bond and McClelland 2021; Bond et al. 2019)? A common pathway to extinction of flightless rails from islands is through predation by introduced predators (Lévêque et al. 2021). The extinction of the Tristan Moorhen is thought to have followed this pathway and have been due to predation by feral cats and hunting for food by islanders using dogs (Beintema 1972; Woolley 1997). Pet cats were removed from Tristan da Cunha in the mid-1970s, leading to the gradual disappearance of the feral population over the next decade. This reduced predation pressure may have allowed the Gough Moorhen to exploit the niche left vacant by the extinction of the Tristan Moorhen, and indeed the historical records we present hint at an increase in the Gough Moorhen population after the 1970s despite being introduced to the island around two decades earlier.

Moorhens occur at higher densities on the Base (6.4 [3.1–13.2] birds/ha) than on the coastal scarp in either woodland (2.9 [1.3–6.3] birds/ha) or Bogfern (4.2 [1.9-9.1] birds/ha) habitats. The Base habitat sampled was between 500 m and 1,000 m elevation, and the preference for this habitat was supported by our elevation model, which predicted a peak population density at around 600 m. Our density estimate for the Base is comparable with the higher end of density estimates for rallids on other oceanic islands (e.g. Inaccessible Island Rail Laterallus rogersi, 6–10 birds/ha; Dilley et al. 2021: Cocos Buff-banded Rail Gallirallus philippensis andrewsi, 3.8-9.9 birds/ha; Woinarski et al. 2016), whilst our scarp habitat estimates are more similar to lower end density estimates from other islands (e.g. Gough Moorhen on Gough Island, 4.6 birds/ha; Watkins and Furness 1986: Henderson Crake Zapornia atra, 2.7 birds/ha; Oppel et al. 2016: Aldabra Rail Dryolimnas cuvieri aldabranus, 1.5-3.0 birds/ha; Hockey et al. 2011). This suggests that the Gough Moorhen population on Tristan da Cunha has reached its carrying capacity and so may be unlikely to increase substantially in the future without changes to the Tristan da Cunha environment; for example the removal of invasive species such as black rats, which are a major agricultural pest and predator of native seabirds on Tristan da Cunha (Dilley et al. 2020). However, our survey did not cover the south-eastern quadrant of the island and so we have assumed that our transects are representative of this southeastern area, extrapolating our population estimate over the entire area of suitable habitat on the island. It is conceivable that densities

could be lower in the south-eastern quadrant of the island, but we believe this is unlikely as this is the least disturbed area on Tristan da Cunha, very seldom visited by islanders, and supports the vast majority of surviving seabirds on the island. This area was already colonised by moorhens by the early 1980s (Figure 2), suggesting that there has been more than enough time for them to reach carrying capacity here.

This is the first formal estimate of the Gough Moorhen population size on Tristan da Cunha and, combined with previous reports of the species' spread across the island, suggests that the population is in a healthy state. As this population was introduced to Tristan da Cunha in the 1950s (Richardson 1984; Woolley 1997), it does not count towards International Union for Conservation of Nature (IUCN) Red List assessments (BirdLife International 2021). Most Gough Moorhens on Gough Island (the species' native range) were killed by primary or secondary poisoning during the 2021 attempt to eradicate mice. The population surviving on Gough Island is unknown but is clearly low as they are not reliably detectable with the standard transect methods previously used on Gough (and in this study), though moorhens are occasionally heard or seen. These occasional detections include juveniles, which shows that the small Gough population is breeding. Should the population on Gough Island fail to recover, our results show that there is a substantial population on Tristan da Cunha that will ensure the species' immediate continued existence. Translocation has been used as a successful conservation tool for island ecosystems (Miskelly and Powesland 2013; Woinarski et al. 2016) and so the moorhen population on Tristan da Cunha could be used as a source population for reintroductions to Gough Island. However, any reintroduction would need to assess the associated disease risk, given the interactions between moorhens and domestic poultry on Tristan da Cunha's Settlement Plain.

Acknowledgements. We thank the Tristan da Cunha Administrator, Island Council, and Conservation Department who provided permission to work on Tristan da Cunha. The 2024 moorhen survey was funded by the Royal Society for the Protection of Birds (RSPB), UK. We thank Andrew Callender, Antje Steinfurth, and Sophie Thomas for logistical support and constructive comments on drafts of this paper. This paper is dedicated to Michael Swales (1930–2024) who was the zoologist on the 1955–1956 Gough Island Scientific Survey.

Supplementary material. The supplementary material for this article can be found at http://doi.org/10.1017/S0959270925100099.

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