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RESEARCH

Life in the slow and high lane: ecology of an alpine gecko (*Mokopirirakau* "Cascades") in the Southern Alps | Kā Tiritiri o te Moana, Aotearoa New Zealand

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Abstract: Alpine regions worldwide support diverse, endemic, and specialised fauna, yet knowledge of the basic ecology of many species is lacking and urgently required for management. Aotearoa New Zealand's lizards (geckos and skinks) are no exception: of at least 33 species that occur in the alpine zone, ≥ 90% are currently Threatened or At Risk of extinction. Here, we focus on the Cascade gecko: a cryptic and viviparous species found in the Southern Alps | Kā Tiritiri o te Moana in the South Island. To improve understanding of its ecology (distribution, habitat use, emergence behaviour, demography, life history, and female reproduction), we collated varied records spanning 50 years and sampled geckos at two alpine sites in South Westland over 46 days, January 2019–March 2023. Of 470 individual geckos reported from 16 sites since 1974, the vast majority (92%, including 334 from our study area) were from the alpine zone. Surveys for lizards (geckos, skinks, or both) in South Westland revealed more geckos with significantly greater catch-per-unit-effort than in Fiordland, possibly due to differences in gecko densities, lithology, terrain, and/or focal taxon surveyed. Consistent with other nocturnally-foraging gecko species that live in cool climates in southern New Zealand, we found evidence for cryptic basking, female-larger sexual-size dimorphism, adult- and female-biased captures, and extended pregnancies. Females in our study area appeared to have summer-to-early-autumn births, pregnancies of ≥ 2 years and triennial reproduction, yielding one of the lowest reproductive outputs reported for female reptiles worldwide. Climate change and predation by introduced mammals are inferred as the main threats to the species. Due to their extremely slow life histories, alpine geckos will require prolonged time-frames for population monitoring and management.

Key words: alpine zone, Diplodactylidae, female reproductive cycle, gestation, lizard.

Introduction

Globally, mountain regions are hotbeds of speciation, supporting diverse, endemic, and specialised biota shaped by geological and climatic processes over deep time (Rahbek et al. 2019; Trewick et al. 2000). Aotearoa New Zealand's alpine zone (defined as the altitudinal belt between the climatic timberline and permanent snowline in summer; Mark et al. 2000) is no exception, supporting at least 33 indigenous lizard species (around a quarter of the nationwide total; Hitchmough et al. 2021) despite comprising only around 11% of the land mass (O'Donnell et al. 2017). The importance of alpine habitats to New Zealand lizards (geckos and skinks) is increasingly recognised via sightings reported to the Department of Conservation (DOC) Herpetofauna Database, research on alpine lizards (Bell et al. 2008; Knox et al. 2019; Bertoia et al. 2021, 2023; Randall et al. 2025) and discoveries of novel taxa that may represent relict populations or obligate alpine species (e.g. Whitaker et al. 2018; Knox et al. 2021; Patterson & Hitchmough 2021).

High-latitude alpine zones, including those found in southern New Zealand, pose unusual thermal challenges for lizards, especially for nocturnal species (Chukwuka et al. 2023). Being ectotherms, lizards rely on external heat sources to regulate their body temperature; thus, all their activities are constrained by climate. Lizards occupying alpine areas may experience large fluctuations in daily temperatures, cold nights, long winters, prolonged snow cover, and heavy rainfall or snow in any season (Bertoia et al. 2021). Further delays in the already slow life histories of many of New Zealand's nocturnal lizard species (including delayed growth and maturation, extreme longevity, and extended pregnancies with less-than-annual reproduction in female geckos; Cree & Hare 2016a) are thus expected to occur in populations inhabiting high-latitude alpine zones, with implications for conservation. As ≥ 90% of the lizard species found in alpine areas are currently Threatened or At Risk of extinction (Hitchmough et al. 2021; O'Donnell et al. 2017), understanding their ecology is vital for the development of effective monitoring and management tools.

Research on nocturnally-foraging gecko species that live

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in cool climates in southern New Zealand has so far revealed a remarkable tolerance for cold nights, with emergence occurring at body temperatures down to 1.4°C (Bertoia et al. 2021; Chukwuka et al. 2023). By day, geckos use thermoregulation to attain elevated body temperatures via postural adjustments within rock retreats (Rock et al. 2002) and cryptic basking (Bertoia et al. 2021; Gibson et al. 2015). An increase in maximum body size and sexual-size dimorphism (SSD) favouring larger females occurs with increasing elevation in kōrero geckos (*Woodworthia* "Otago large") from Otago (Penniket & Cree 2015; Cree & Hare 2016a). Extended pregnancies (up to 14 months) with biennial reproduction have been documented in females from a sub-alpine population (c. 700 m a.s.l.) of this species (Cree & Guillette 1995), and less-than-annual reproduction is also found in female orange-spotted geckos (*Mokopirirakau* "Roy's Peak") in the Otago alpine zone; Knox et al. 2019). Whether the above traits apply to New Zealand's alpine geckos generally remains unknown, as research on other species and populations in other alpine regions is lacking.

The Cascade gecko (*Mokopirirakau* "Cascades"; nomenclature of Hitchmough et al. 2021) is a cryptic, viviparous (live-bearing), and undescribed diplodactylid gecko species that inhabits the Southern Alps | Kā Tiritiri o te Moana, South Island. It is primarily known from alpine areas (DOC Herpetofauna Database 2024) and has a conservation status of At Risk – Declining under the New Zealand Threat Classification System (NZTCS; Hitchmough et al. 2021). Similarly to other alpine geckos in New Zealand, the most recent NZTCS assessment for this taxon includes "Data Poor Trend" and "Climate Impact" qualifiers (Hitchmough et al. 2021; Rolfe et al. 2021). This is because population trends have not yet been assessed in any New Zealand alpine gecko population. Population trends are difficult to assess in alpine geckos due to a lack of robust monitoring tools and the lengthy (> 10 year) time-frames needed to obtain meaningful results. Alpine geckos are expected to be negatively affected by a warming climate over the long term (Hitchmough et al. 2021; Jarvie et al. 2022 but see Chukwuka et al. 2023).

Here, we summarise ecological data and knowledge of Cascade geckos, based on records from varied sources spanning 50 years and our own research conducted at two alpine sites in South Westland over five field seasons (February 2018–March 2023). Specifically, we document: (1) the species' discovery, broad habitat use, and distribution; (2) encounter rates in Fiordland and South Westland, the two main regions where it is found; (3) aspects of its life history and behaviour (including cryptic diurnal basking, population demography, SSD and the female reproductive cycle observed in our study area); and (4) inferred threats. This paper provides the first population-level study for Cascade geckos and adds to the scant ecological literature available for New Zealand's alpine geckos (at least 13 taxa; O'Donnell et al. 2017; Knox et al. 2019; Bertoia et al. 2021; Randall et al. 2025).

Methods

Review of existing information

We collated and reviewed potential and verified records of Cascade geckos, sourced from the DOC Herpetofauna Database (accessed 5 June 2024), species-identification application iNaturalist NZ (research-grade observations only; https://inaturalist.nz/), published and unpublished surveys and observations dating back to 1974, and our own research. To verify survey data and solicit additional sightings, we also contacted herpetologists and DOC personnel who had conducted lizard surveys within the species' geographic range. Records of unidentified geckos in the DOC Herpetofauna Database were assumed to be Cascade geckos if subsequent surveys conducted nearby located at least one Cascade gecko that had its identity confirmed via mitochondrial DNA (ND2 gene) sequence analysis (R. Hitchmough, DOC, Wellington, pers. comm.). No other gecko taxa are known to occur within the species' range. The resulting data were used to generate a broad-scale distribution map. Geographic range size was conservatively estimated from a polygon drawn in Google Earth Pro, using the straight-line distances between all verified peripheral records.

All relevant data, including observation dates and times, gecko locations, behavioural observations, elevations, and habitat descriptors, were collated. Sites were defined using catchment boundaries and/or landforms, where multiple records from continuous habitat on one mountain range were counted as one site. We calculated a basic index of abundance, catch-per-unit-effort (CPUE; number of geckos found divided by the number of person-hours spent searching) for surveys where such data were available. A two-sample t-test was used to compare CPUE for lizard surveys conducted in South Westland versus Fiordland. Although the species is also found in far western Otago (DOC Herpetofauna Database 2024), there were insufficient data to permit comparison to this region. As: (1) some surveys targeted alpine skinks with geckos reported as by-catch (they are sympatric and share crevices in some areas; e.g. Bell et al. 2008), (2) detectability can vary with the terrain, and (3) a proportional relationship between CPUE and abundance has not been demonstrated for alpine geckos, we acknowledge that CPUE is only broadly indicative of the ease of encountering geckos and may not reflect densities.

Study sites

We sampled geckos at two locations c. 5 km apart on a mountain range in South Westland, South Island, on 46 days between February 2018 and March 2023 (six field seasons). Throughout, we refer to the mountain range as our study area and our sampling sites as Site A and Site B (locations are not disclosed here to reduce the risk of illegal collection of geckos). Gecko habitat at both sites consisted of schist boulder fields in tall tussock (*Chionochloa* sp.) grasslands at elevations of c. 1050–1500 m a.s.l. (Fig. 1). The sites lie in a region where the median annual mean air temperature is around 7°C and median annual rainfall ≥ 6000 mm (Macara 2016).

Sites were accessed by teams of 2–5 observers in favourable weather (typically, 3–4 day periods of predominantly fine weather with little or no rainfall, light winds, and daily temperature maxima ≥ 10°C). Site A was sampled on 12 days over 15 months (6–9 February, 6–9 March, and 26–28 November 2018, and 30 April 2019). Site B was sampled on 34 days over 50 months (10–14 January and 24–26 December 2019; 7–9 February and 13–15 December 2020; 11–13 January, 11–13 March, and 23–25 December 2021; 13–15 March and 27–29 December 2022; and 11–13 January and 21–23 March 2023). Sampling effort varied among field trips and years due to weather, research priorities, and the number of observers. For comparison of CPUE to other sites, we used data from the first three surveys of each study site only, as increasing site familiarity could inflate gecko encounter rates over time.

Figure 1. A Cascade gecko (*Mokopirirakau* “Cascades”; posed individual; Photo: T. Gunn) and its habitat in our study area.

Geckos were located by day-time rock lifting and inspection of rock crevices using a small torch, and captured by hand where possible. Overturned rocks were carefully returned to their original positions. All captured geckos were measured (snout–vent length (SVL), vent-tail length, and the length of any tail regeneration; all to the nearest mm using a clear plastic ruler), sexed (mature individuals only; by the presence of a hemipenial sac and enlarged cloacal spurs in males, and absence of these structures in females), and weighed to the nearest 0.1 g using a Pesola© spring balance. A Kestrel 3000 hand-held weather meter was used to measure ambient (shade air) temperatures at approximately 1.3 m above ground.

The abdomens of mature females were gently palpated (Cree & Guillette 1995) to infer clutch size and reproductive status (in five stages: non-reproductive, vitellogenic, early-pregnant, mid-pregnant, or late-pregnant, based on the size and shape of vitellogenic follicles or embryos). All geckos with SVLs ≥ the smallest reproductive female found in our study area were categorised as adults. The dorsum of each gecko was photographed to enable individual identification via photo-identification (as for other *Mokopirirakau* species; Hoare et al. 2013; Romijn et al. 2014; Knox et al. 2019). Targeted searching for adult females that had been captured on preceding field trips was carried out at Site B from January 2021 onwards to define the timing of births, gestation length, and frequency of reproduction. The latter was primarily inferred from the palpation data of a subset of 12 females, each caught at least three times in consecutive ($n = 9$) or non-consecutive ($n = 3$) field seasons. Although we had no reason to expect differences in adult size distributions or sex ratios between study sites, we used separate two-tailed t-tests to first assess whether mean adult SVL differed by site (pooling the data after no significant difference was found) and then sex (a test for SSD). The adult size threshold was SVL ≥ 70 mm, based on the smallest reproductive female in our dataset (a pregnant female). A Chi-square test was used to compare adult sex ratios between sites. All results were considered significant at $\alpha = 0.05$. Unless stated otherwise, data from recaptured geckos were excluded from analyses.

Results

Gecko observations over 50 years: from species discovery to current knowledge

In March 1974, then-Wildlife Service Ranger Rod Morris encountered a juvenile gecko in sub-alpine scrub (in *Podocarpus nivalis*) while searching for kākāpo (*Strigops habroptilus*) by day in a remote Fiordland valley. It was collected and identified as an unusual forest gecko (*Mokopirirakau granulatus*) that warranted further investigation (R. Hitchmough, DOC, Wellington, pers. comm.). Due to a lack of mature specimens available for further study, 25 years passed before it was recognised as a novel taxon; the latter was achieved by morphological comparison to three adult geckos found in South Westland in 1999 (R. Hitchmough, DOC Wellington, pers. comm.; DOC Herpetofauna Database 2024). The species was first evaluated under the NZTCS in 2002, being ranked then as "Data Deficient" (Hitchmough 2002).

In contrast to the dearth of data from the quarter-century after the species' discovery, gecko sightings have increased steadily in the last 25 years, with 60, 119, and 286 individuals reported from 2000–2009, 2010–2019, and 2020 onwards, respectively. In total, we located records for 470 geckos from 16 sites at elevations of 160–1720 m a.s.l. within a c. 450 000 ha area in Fiordland, South Westland, and west Otago (Fig. 2; Appendix S1 in Supplementary Material). This included 334 individuals (71% of the total number of geckos reported) from our study area, excluding data from 77 geckos that could not be individually identified because they were unable to be caught (either because they were in deep crevices or evaded capture). Geckos were rarely reported from non-alpine habitats ($n = 36$ individuals from six sites; 7.7% of the total reported), with most of those ($n = 33$) being from ancient moraine ridges with sparse and stunted vegetation due to the high ultramafic content of the basement rocks (Sutherland et al. 1995). In such areas, geckos were encountered by day (under rocks, in crevices and in Onduline retreats; DOC Herpetofauna Database 2024), with one gecko observed basking in the late morning, while others were seen emerged at night in areas of bare rock (M. Tocher, Lizard Expert NZ, Dunedin, pers. comm.). There was also one record each from sub-alpine scrub (the aforementioned Fiordland juvenile) and forest: a gecko found inside a tent pitched on a river terrace surrounded by podocarp forest at 300 m a.s.l. (accidental transport was ruled out; DOC Herpetofauna Database 2024).

Notably, climbers and trampers (hikers) reported ten gecko sightings (2.1% of the total number reported), all encountered by day in alpine areas: eight were seen in crevices on steep rock walls, cirques, and peaks in Fiordland, and two were reported from a walking track in Otago (DOC Herpetofauna Database 2024). Overall, geckos were most often found under rocks by day, but one survey of a c. 1600 m peak on the Main Divide reported only night-time encounters despite utilising multiple methods (day searching, spotlighting, and funnel traps; T. Bell, Wildland Consultants Ltd., Wellington, pers. comm.).

ExpertGPS Basemap: mapbox, OpenStreetMap

Figure 2. Distribution of Cascade geckos (*Mokopirirakau* "Cascades"), South Island, New Zealand.

In that survey, nine emerged geckos were found by spotlighting over two nights in early autumn at air temperatures of 6.7–10.1°C (T. Bell, Wildland Consultants Ltd., Wellington, pers. comm.). In contrast, the first gecko sighted on that peak was partially exposed and basking by day, retreating under a rock when accidentally disturbed (T. Rawlence, Department of Conservation, Nelson, pers. comm.).

On average, lizard surveys conducted in South Westland located more geckos (mean = 25.1 ± 5.49 [SE]) than those in Fiordland (2.8 ± 0.52 geckos) with significantly greater CPUE ($t = 2.13$, $p < 0.05$) (Fig. 3; Appendix S1). However, eight of the 11 Fiordland lizard surveys for which we had CPUE data targeted alpine skinks, with geckos reported as by-catch only (e.g. Bell et al. 2008). In contrast, all but three of the 13 South Westland surveys targeted geckos and rarely reported skinks (DOC Herpetofauna Database 2024).

Findings from our study sites

In total, we obtained 388 daytime captures of 310 Cascade geckos in our study area: 87 from Site A and 223 from Site B. Geckos found under rocks were mostly solitary, but there were two sightings of adult male/female pairs, one of an adult female with another adult that evaded capture, and six encounters with juvenile/adult pairs (adults were of both sexes). Daytime observations of geckos engaged in apparent thermoregulation behaviour included a male basking in a shallow rock crevice with his head and flanks in the sun, a female moving under a rock on approach, a female half-emerged from plate rock under a thin surface rock, and a female sitting in a sun-warmed black alkathene pipe (0.5 m × 5 cm) used to record gecko tracks. In addition, we occasionally saw juveniles and adults under rocks that had been checked earlier in the day without finding geckos, and usually when rocks were cold and/or in the shade. Geckos were caught at ambient air temperatures of 4.7–23.7°C, with 95% of captures for which we had data occurring between 7.8°C and 20.8°C ($n = 360$).

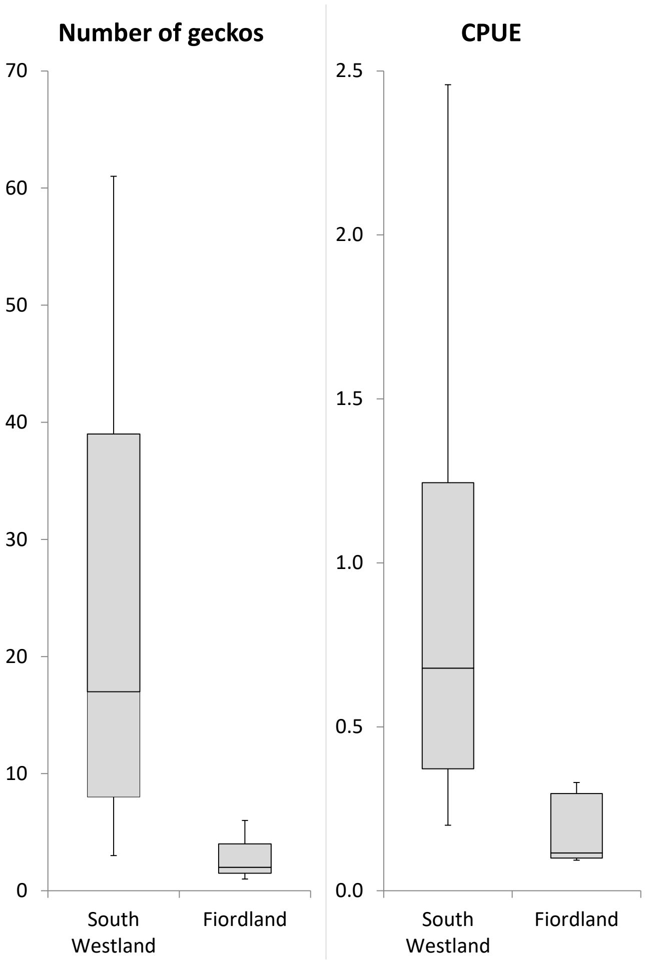

Figure 3. Numbers of Cascade geckos and catch-per-unit-effort (CPUE; median, lower and upper quartiles, minimum and maximum) for lizard surveys conducted in South Westland (n = 13) and Fiordland (n = 11), February 1999–March 2023. Survey duration ranged from <1–4 days (Appendix S1). CPUE was calculated by dividing the number of geckos found (including escapes) by the number of person-hours spent searching (where such data was available; Appendix S1). Regional differences in CPUE were significant ($P < 0.05$; see text).

Geckos ranged in size from 36–95 mm SVL. We did not encounter any clearly identifiable neonates (newborn geckos). The smallest individuals that were confidently identified as male and female had SVLs of 61 and 65 mm, respectively. The smallest female that contained reproductive structures (two embryos) had an SVL of 70 mm. Mean SVL did not significantly differ between sites ($t = -0.822$, $p = 0.41$); thus, size data were pooled for further analysis. Females reached larger body sizes (maximum SVL = 95 mm) than males (maximum SVL = 89 mm) (Fig. 4). Adult mean SVL was significantly larger in females (81.5 ± 0.46 [SE] mm) than males (79.0 ± 0.47 mm; $t = 3.65$, $p < 0.001$). Adult females were caught in greater numbers than adult males (♀:♂; Site A = 51:17, a ratio of 3:1; Site B = 91:69, a ratio of 1.3:1), in proportions that differed significantly by site ($\chi^2 = 6.67$, $p < 0.05$) and deviated strongly from a 1:1 sex ratio ($\chi^2 = 20.03$, $p < 0.0001$). We captured fewer juveniles than adults (Site A = 19 juveniles:68 adults, Site B = 63 juveniles:160 adults).

At Site B, none of the nine adult females that were captured in three consecutive field seasons (a period of around 2 years) had completed an entire reproductive cycle within that time, suggesting it takes study females 3 years or longer to produce a single clutch (Table 1). Two of these females are known to have been continuously pregnant for c. 24 months (i.e. they contained embryos that increased in size over time, as inferred by abdominal palpation, without any evidence of births occurring between captures). As we were not able to observe females with newborns, we assumed that births had occurred if late-pregnant females became post-partum (evident from loose abdominal skin), non-reproductive, or contained small vitellogenic follicles on subsequent captures made within the same field season. Four females gave birth between successive captures in the same season, two between late December and early February, and two between mid-December and mid-March. Three additional females caught in three non-consecutive seasons had reproductive data that were consistent with a triennial cycle (e.g. near-completion of one entire cycle over 1078 days (2.95 years) for Gecko 10; Table 1). No females were caught in more than three consecutive seasons; thus, we were unable to observe the full reproductive cycle in any individual. Mean, median, and maximum clutch sizes were 1.96, 2, and 2, respectively ($n = 82$ pregnant females; first captures only).

Finally, geckos displayed striking variability in colouration and markings (Fig. 5), and frequently altered their base body colour within minutes of capture. Although body colour was not constant, the shapes and relative positions of the dorsal markings remained stable over time, thereby permitting accurate individual identification over the study period.

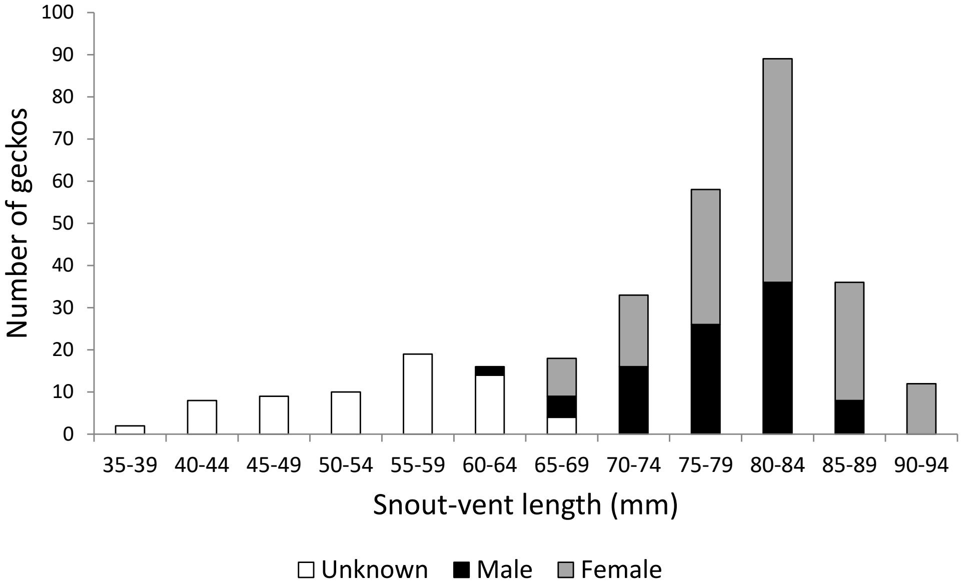

Figure 4. Size-class distribution of geckos (first captures only) from our study area in South Westland. The maximum SVL of 95 mm, observed in a recaptured female, is not shown.

Discussion

Geographic range, habitat use, CPUE, and emergence activity

Cascade gecko encounters spanning 50 years have improved understanding of the ecology of this small, cryptic inhabitant of the Southern Alps | Kā Tiritiri o te Moana. The species appears to be sparsely distributed over a large (c. 450 000 ha) mountainous area, with the vast majority of records originating from rocky habitats at high elevations and high latitudes (c. 44°0′–45°15′S). In addition to the thermal challenges this creates for a small viviparous ectotherm, Cascade geckos also inhabit the wettest part of Aotearoa, with annual rainfalls exceeding 8000 mm and 6000 mm in western Fiordland and South Westland, respectively (Macara 2013, 2016). The known geographic range may change, as preliminary results from nuclear DNA analysis using genotyping-by-sequencing techniques have recently revealed that the species boundaries for several *Mokopirirakau* spp. geckos in South Westland do not match those currently recognised (S. Walters, University of Otago, Dunedin, pers. comm.).

CPUE was significantly greater for surveys undertaken in South Westland compared to those in Fiordland, potentially reflecting differences in gecko densities, lithology, the accessibility of the terrain, and/or focal taxon (gecko, skink, or both). Although gecko detectability has not been formally estimated at any site, we have found Cascade geckos easier to locate in schist boulder fields and ultramafic areas in South Westland than in the deep crevices and rock jumbles they tend to occupy on sheer gneiss and diorite bluffs in Fiordland. Assistance from climbers was vital to the success of the first surveys conducted in Fiordland: climbers reported the first Cascade gecko and alpine skink encounters from some remote locations (DOC Herpetofauna Database 2024), provided roped access to allow safe capture and identification of lizards by herpetologists in steep terrain (Bell et al. 2008), and discovered novel species (e.g. Barrier skink *Oligosoma judgei*; Patterson & Bell 2009).

Surprisingly, there was only one Cascade gecko reported from forest despite temperate forest being the dominant habitat at lower elevations throughout the species' range. This low number could be due to a survey bias favouring alpine areas, and/or lower detectability or density of geckos in forest. Geckos living in tall, closed-canopy forest are notoriously difficult to detect (Lettink & Monks 2016; but see Turner et al. 2024 for improved tools). They are exposed to a suite of introduced mammalian predators that have been the primary cause of widespread declines in indigenous forest birds (Innes et al. 2010), and of range contractions and extinctions in the New Zealand herpetofauna (Towns & Daugherty 1994). Ngahere geckos (*Mokopirirakau* "Southern North Island") that were radio-tracked in an urban forest spent long periods of time emerged on trunks and branches, both by day and night, and infrequently used retreats, leading Romijn et al. (2014) to speculate that this exposed behaviour may increase their vulnerability to predation by foraging mammals. Cascade geckos living in forest could be using the epiphytic canopy as habitat, as suggested by a video camera study that revealed gecko activity (presumed to be from a single *Mokopirirakau granulatus*) within a nest epiphyte (*Collospermum hastatum*) in the Waitakere Ranges (Henwood et al. 2014).

Based on observations of nocturnal emergence and diurnal activity in Cascade geckos, and similar behaviour in other *Mokopirirakau* species (Romijn et al. 2014; Bertoia et al. 2021), we conclude that Cascade geckos are diurno-nocturnal (Werner & Whitaker 1978). Our limited evidence for diurnal activity in Cascade geckos is unsurprising given that 64% of the 33 nocturnally-foraging gecko species in New Zealand have been observed emerged and basking by day (Rock et al. 2002; Gibson et al. 2015; Hare et al. 2016; Bertoia et al. 2021). Researchers have speculated that viviparous lizards in cool climates may not ever be strictly nocturnal (Gibson et al. 2015) and that foraging could also occur by day (Romijn et al. 2014). We expect greater diurnal activity in alpine versus lowland Cascade gecko populations, a prediction that could be tested in the field using time-lapse trail cameras (thereby eliminating any effect of observer presence; Bertoia et al. 2021; Chukwuka et al. 2023).

Additional population insights from our study area

Consistent with research on other cool-climate geckos from southern New Zealand (Cree & Guillette 1995; Penniket &

Table 1. Reproductive data for 12 adult female geckos caught in three consecutive field seasons (first nine geckos) or three non-consecutive field seasons (last three geckos) at Site B, January 2019–March 2023. Reproductive status was inferred by abdominal palpation (see text): NR = non-reproductive (no vitellogenic follicles or embryos detected), V = vitellogenic, EP = early pregnant, MP = mid-pregnant, LP = late pregnant. Also indicated are the numbers of follicles or embryos detected and whether embryos had discernible form.

Gecko ID	Date	Field season	Observation period	Reproductive status	Notes
1	10-Jan-19	1	705 days (1.93 y)	EP × 2	
	9-Feb-20	2		LP × 2 (no form)	
	15-Dec-20	3		LP × 2 (form felt)	Has been continuously pregnant for almost 2 y
2	14-Jan-19	1	788 days (2.16 y)	LP × 2 (no form)	
	24-Dec-19	2		LP × 2 (no form)	
	9-Feb-20	2		LP × 2	
	13-Dec-20	3		LP × 2 (form felt)	
	12-Mar-21	3		V × 1	Birthed since last capture
3	24-Dec-19	2	811 days (2.22 y)	V × 2	
	12-Mar-21	3		LP × 2 (no form)	
	24-Dec-21	4		LP × 2 (no form)	
	14-Mar-22	4		LP × 2 (no form)	
4	26-Dec-19	2	808 days (2.21 y)	Mid-late P × 2	
	15-Dec-20	3		LP × 2 (form felt)	
	13-Mar-22	4		EP × 1	Birthed since last capture
5	9-Feb-20	2	763 days (2.09 y)	LP × 2 (no form)	
	12-Jan-21	3		LP × 2 (form felt)	
	11-Mar-21	3		NR	Birthed since last capture
	13-Mar-22	4		EP × 2	
6	9-Feb-20	2	683 days (1.87 y)	NR	No follicles detected, feels flat – recent birth?
	12-Jan-21	3		MP × 2	
	23-Dec-21	4		LP × 2 (no form)	
7	9-Feb-20	2	764 days (2.09 y)	MP × 2	
	13-Dec-20	3		LP × 2 (form felt)	
	13-Jan-21	3		LP × 2 (form felt)	
	12-Mar-21	3		LP × 2 (form felt)	
	14-Mar-22	4		EP × 2	Birthed since last capture
8	15-Dec-20	3	826 days (2.26 y)	MP × 2	
	11-Jan-21	3		MP × 2	
	23-Dec-21	4		LP × 2 (no form)	
	13-Mar-22	4		LP × 2 (form felt)	
	28-Dec-22	5		V × 2	Birthed since last capture
	21-Mar-23	5		EP × 2	
9	15-Dec-20	3	743 days (2.04 y)	LP × 2 (form felt)	
	11-Mar-21	3		V × 2	Birthed since last capture
	23-Dec-21	4		EP × 2	
	13-Mar-22	4		EP × 2	
	28-Dec-22	5		MP × 2	
10	12-Jan-19	1	1078 days (2.95 y)	NR	
	26-Dec-19	2		EP × 2	
	25-Dec-21	4		LP × 2 (form felt)	No yolk mass felt; appears ready to birth.
11	12-Jan-19	1	1446 days (3.96 y)	LP × 2 (no form)	
	24-Dec-19	2		LP × 2 (form felt)	
	9-Feb-20	2		V × 2	Has birthed since last capture. Tiny follicles, still looks pregnant.
	28-Dec-22	5		V × 1	Baggy flanks, recent birth? Tiny follicle on right side, nil felt on left.
12	25-Dec-19	2	1098 days (3.01 y)	LP × 2 (no form)	
	25-Dec-21	4		MP × 2	Birthed since last capture
	27-Dec-22	5		LP × 2 (no form)	

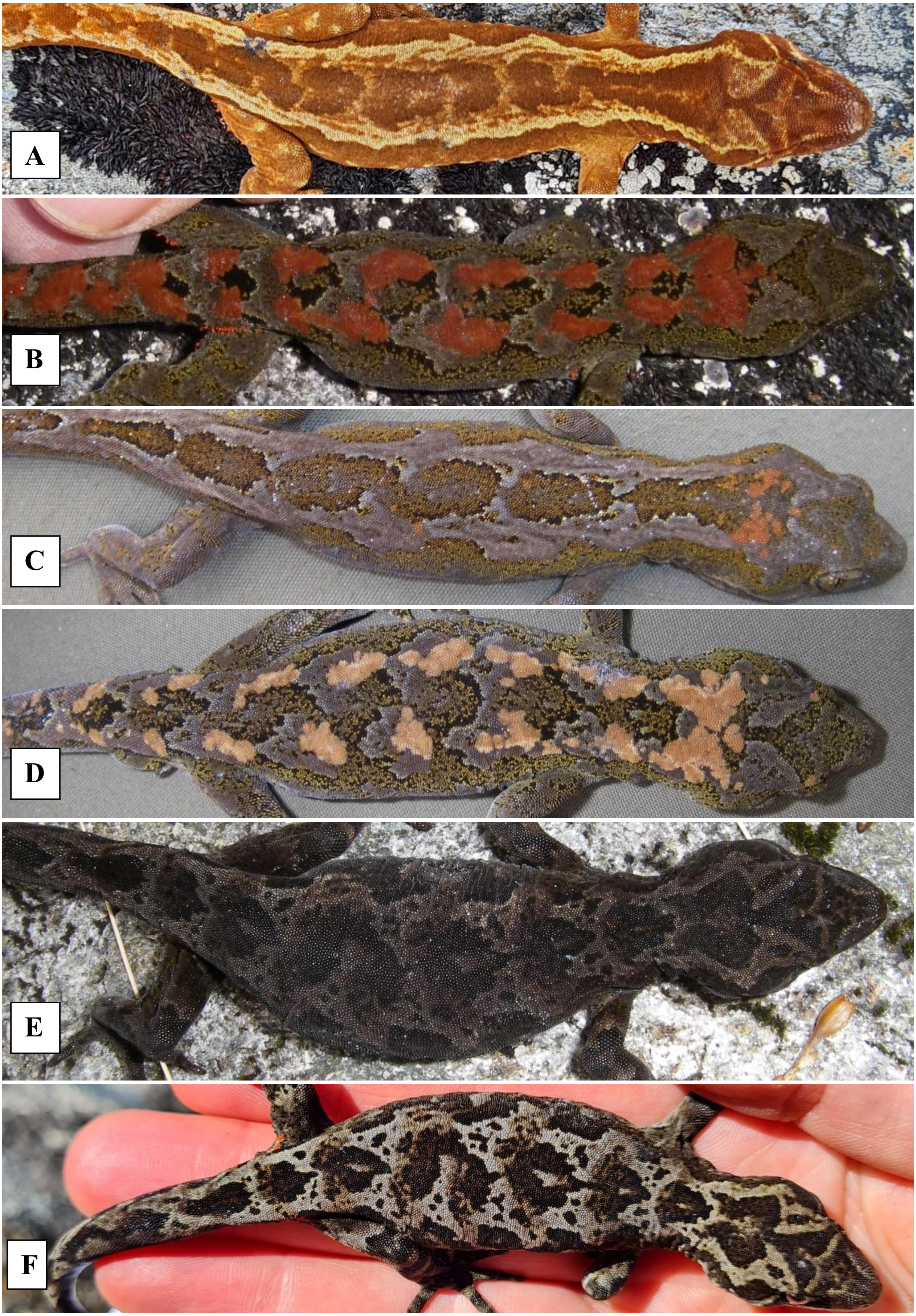

Figure 5. Variability in dorsal markings and colouration of Cascade geckos including two images of the same individual (E & F; photographed 808 days apart) to show colour changes.

Cree 2015; Cree & Hare 2016a; Knox et al. 2019; Bertoia et al. 2021), we found significant female-larger SSD, female-biased captures, fewer juveniles than adults, and extended pregnancies with less-than-annual reproduction in female Cascade geckos. In addition, we report infrequent sharing of diurnal rock retreats with conspecifics. We discuss the relevance of each of these findings below.

Firstly, we found significant SSD favouring larger females. Globally, males of most lizard species are larger than females, but species with female-biased SSD are found in nearly all families (Cox et al. 2007), most often in viviparous lineages with infrequent female reproduction (Liang et al. 2022). Female-biased SSD occurs in other geckos from southern New Zealand (Cree & Hare 2016a; Knox et al. 2019) and lizards from high-latitude sites elsewhere (Fernández et al. 2015; Tarr et al. 2019; Valdecantos et al. 2019). This pattern is presumed to have evolved to maximize fecundity (Darwin 1874). We speculate that it may enable larger Cascade gecko females to produce larger offspring with increased survival in cool climates. Given that reproductive output is constrained by temperature and geckos have an ancestrally-fixed low clutch size (maximum of two; Sakai 2021, but see Meiri 2019), alpine geckos cannot increase their fecundity by increasing breeding frequency or clutch size.

Secondly, we captured more adults than juveniles, and more adult females than males, likely reflecting differences in detectability between age- and sex-classes. We had no means to quantify the true (cf. observed) ratios, but spotlighting (Whitaker 1967) could be used to compare sex and age ratios in geckos emerged at night. We suspect that adult females are more detectable by day because they spend more time under superficial rocks to elevate their body temperatures, thereby hastening embryonic development. A relationship between maternal basking opportunity and gestation length has been experimentally demonstrated: early-pregnant kōrero geckos sourced from the wild and given variable basking regimes in a laboratory had mean gestation lengths that ranged from around 6 months (178 days) under the warmest regime to around 7.4 months (223 days) under the coolest regime (Cree & Hare 2016b). In addition, offspring birthed by females in the coolest basking regime were smaller than those in other groups, but did not have reduced survival.

Thirdly, our study females appear to have ≥ 2-year pregnancies and triennial reproduction with summer-to-early-autumn births, but these inferences were limited by a small sample size and the use of an indirect method for inferring reproductive stage. Dissection to independently verify the accuracy of abdominal palpation (Cree & Guillette 1995) was not justified given the species' threat status. However, preliminary results from our recent attempts to verify the accuracy of our palpation technique via ultrasonography were consistent. Due to low detectability and recapture rates, we were unable to conduct annual palpation for the full reproductive cycle (i.e. from vitellogenesis to birth) in any female, and therefore we base our evidence for triennial reproduction on the collective data obtained for 12 females from Site B, for which we had frequent captures spanning five field seasons.

With a mean clutch size of 1.96 and inferred triennial reproduction, annual reproductive output (ARO; mean number of offspring/female/year; Cree 1994) of females in our study population is 0.65; amongst the lowest values reported for female reptiles worldwide (Cree & Hare 2016a; Meiri et al. 2021). As the possibility of a longer cycle and/or less-frequent reproduction occurring in some females cannot be excluded, an ARO of 0.65 may be an over-estimate. Regardless, single clutches were rare and years of skipped reproduction have not been observed; both occur in female reptiles from cool-climate populations elsewhere (Ibargüengoytía & Casalins 2007; Boretto et al. 2014; Rutherford & Gregory 2023), presumably due to climatic constraints. Triennial reproduction has not previously been documented in New Zealand reptiles, but its possibility has been raised for other southern geckos, namely orange-spotted gecko (Knox et al. 2019) and harlequin gecko *Tukutuku rakiurae* (M. Tocher, Lizard Expert NZ, Dunedin, pers. comm.).

We were unable to determine age at first breeding in females or longevity due to low recapture rates (particularly for juveniles) and the short study duration relative to the lifespan of New Zealand geckos (e.g. 50+ years (Cree & Hare 2016a), though recent findings indicate that lifespans can exceed 60 years; ML/DOC, unpubl. data). As female kōrero geckos living at elevations of around 700 m a.s.l. in Otago take 8 years to reach sexual maturity (Cree & Hare 2016a) and have pregnancies of up to 14 months with biennial reproduction in some females (Cree & Guillette 1995), it is not unreasonable to surmise that female Cascade geckos living at around double the elevation with ≥ 2-year pregnancies and triennial reproduction may take a decade or more to breed for the first time.

Finally, in contrast to refuge-sharing and social aggregations common in some geckos (Kearney et al. 2001; Hare et al. 2016; Chukwuka et al. 2021), Cascade geckos were mostly solitary in daytime retreats, occasionally sharing them with one other individual, but never observed in groups. Other *Mokopirirakau* spp. geckos have occasionally been seen sharing daytime retreats in small numbers (up to three individuals; Hoare et al. 2013). We also observed different individuals (males, females, and juveniles) using the same rocks at different times. Romijn et al. (2014) similarly found that radio-tagged ngahere geckos were almost never seen together but used the same crevices as conspecifics at different times. Occasional refuge-sharing in *Mokopirirakau* spp. geckos may be for social reasons, or due to the refuges being in short supply or of unusually high quality (Kearney et al. 2001).

Threats

As Cascade geckos are well-represented on Public Conservation Land (where risk of habitat destruction is generally low), we infer climate change and introduced mammalian predators to be the main threats to the species. Although alpine areas may support fewer mammalian predators and a subset of the species found below the tree line, the ten species that occur there are known to have adverse, albeit poorly-understood, impacts on indigenous fauna (O'Donnell et al. 2017). Stoats (*Mustela erminea*), ship rats (*Rattus rattus*) and house mice (*Mus musculus*) are likely to be the main predators of Cascade geckos in the alpine zone, based on rodent tracking rates, predator trap-catch data, and gecko remains found in the gut of a freshly-killed stoat (O'Donnell et al. 2017). Landscape-scale suppression of stoats is undertaken at some sites to protect populations of threatened birds (Weston et al. 2018), but this may not benefit, and could possibly harm, geckos if it results in increased predation by (unmanaged) mice via meso-predator release (Norbury et al. 2023; Monks et al. 2024).

Worldwide, more than half (52.1%) of reptile species face an increased risk of extinction from climate change (Li et al. 2024). The species' ranges of most New Zealand lizards, including geckos at high elevations, are predicted to decrease due to the direct effects of climate change (Jarvie et al. 2022), but potential benefits to cool-climate geckos include increased nocturnal activity, particularly in autumn and winter (Chukwuka et al. 2023) and reduced gestation length (potentially shifting the birth season forward; Moore et al. 2020).

As the Cascade gecko's range is predicted to become warmer and wetter, and experience more days with extreme rainfall (Ministry for the Environment [MfE] 2018), direct benefits of climate change seem unlikely. Because the moisture-holding capacity of air increases with ambient temperature, any potential gains from increased temperatures may be offset by increased precipitation and cloud cover, both of which reduce day-time basking opportunities for lizards (Hare & Cree 2010). In addition, a rising snowline and reduced seasonal snow cover (MfE 2018) will permit upward shifts in the elevational ranges of introduced mammalian predators (Walker et al. 2019; Foster et al. 2021; Harris et al. 2022). Other indirect effects of a warming climate on alpine geckos may include more frequent predator irruptions driven by increased snow tussock (*Chionochloa* spp.; Wilson & Lee 2010; Monks et al. 2016) and beech mast seeding events (Christie 2014; O'Donnell et al. 2017; Macinnis-Ng et al. 2021).

Alpine reptiles are inherently more vulnerable to threats than their lowland counterparts due to the slower rates at which they are able to grow, mature and reproduce (Boretto et al. 2018). Due to their extremely slow life histories, Cascade and other alpine geckos will require extended time-frames for monitoring population trends and responses to conservation management actions. This will need to be factored into conservation planning.

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Ethics: All fieldwork was conducted under DOC Wildlife Act Authority Numbers 35196-FAU and 71046-FAU held by ML.

Data availability: Gecko locations are not disclosed here to reduce the risk of illegal collection of geckos. The data used in this paper can be accessed on reasonable request by contacting the corresponding author.

Author contributions: ML and JM designed the study and collected the data. ML wrote the manuscript and conducted the data analysis, with editorial contributions from JM & AC.

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Supplementary Material

Additional supporting information may be found in the online version of this article.

Appendix S1. Collated gecko survey data from throughout the species' range.

The New Zealand Journal of Ecology provides online supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.