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RESEARCH ARTICLE

Camera-trapping density estimates suggest critically low population sizes for the Wet Tropics subspecies of the spotted-tailed quoll (*Dasyurus maculatus gracilis*)

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Abstract

Accurate estimates of distribution and population density are critical for the management of threatened species. This is particularly pertinent for mammalian predators, whose generally low population density, elusive nature, and large home range requirements make it difficult to detect declines. We aimed to refine population estimates of the northern spotted-tailed quoll (*Dasyurus maculatus gracilis*) in the Wet Tropics bioregion, to estimate the total number of adults, the likely size of subpopulations across the known distribution of the subspecies, and its associated conservation status. We performed targeted upland camera-trapping surveys from June 2017 to May 2019. To calculate population densities, we used a combination of the number of individuals identified from each survey and the mean maximum distance moved from three life history stages. We then extrapolated these estimates to modelled suitable habitat areas, refined by the camera-trapping surveys. Population sizes for the six defined subpopulations were estimated, and ranged from approximately 5 to 105 individuals. The total population was estimated to be 221 individuals. This total population estimate, and the estimates for each of the subpopulations, are lower than previous published estimates and are cause for concern. Given the low population estimates presented here and unresolved threats driving declines in some subpopulations, we suggest elevation of this subspecies to Critically Endangered under the EPBC Act.

KEYWORDS
endangered, marsupial, population size, predator, upland

INTRODUCTION

Estimating population density and/or population size of threatened species at points in time is essential for detecting and quantifying population changes (Robinson et al., 2018). Targeted surveys and monitoring are important for cryptic and low-density species, such as mammalian predators, which means using the best methodology for detecting that species and applying it to as many of their known populations as possible (Ceballos et al., 2017; Ripple et al., 2014; Robinson et al., 2018). Whilst targeted surveys may come at the cost of optimal accuracy of population estimates at any one site (Stewart et al., 2021), they can ultimately generate data across the distribution of the species to capture variation in population density, which may be explained by associations with environmental variation as well as potential threats.

Camera trapping is an effective technique for estimating population sizes of uniquely marked species such as quolls, in which individual recognition enables the use of mark-recapture techniques (Silver et al., 2004; Blanc et al., 2013; Nelson et al., 2014). Methods for estimating density of these rare species include techniques to determine the effective trapping area (ETA), such as mean maximum distance moved (MMDM) and capture–recapture modelling methods such as spatially explicit capture–recapture (SECR) models (Foster & Harmsen, 2012; Rovero et al., 2013). Camera trapping, coupled with these techniques, has been successfully used to estimate the population density and size of elusive mesocarnivores, such as wolverines (Stewart et al., 2016) and larger carvnivores (e.g. *Panthera pardus*, *P. leo*) (Balme et al., 2009; O'Brien & Kinnaird, 2011), where these population data may lead to the improved ability to detect declines through time (Rich et al., 2017).

The spotted-tailed quoll (*Dasyurus maculatus*) is the largest extant marsupial carnivore on mainland Australia (Belcher et al., 2008) and is recognized as two subspecies: *D. m. maculatus*, in south-east mainland Australia and Tasmania, and *D. m. gracilis* in north-east Queensland. *Dasyurus m. gracilis* is restricted to the Wet Tropics bioregion, where it occurs in upland rainforest and adjacent tall wet sclerophyll forest (Burnett, 2001; Uzqueda et al., 2020). The subspecies is listed as Endangered under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act). Potential threats for *D. m. gracilis* are habitat loss and fragmentation, persecution, roadkill, poisoning from invasive cane toads (*Rhinella marina*), and climate change; however, the cause of contemporary declines remains unresolved (Burnett & Marsh, 2004; Uzqueda et al., 2020). Resolving the persistence of subpopulations and estimating their sizes have been recognized as priorities for management (DEWLP, 2016; Uzqueda et al., 2020).

Since the late 19th century, four subpopulations of *D. m. gracilis* have disappeared (Burnett & Marsh, 2004; Uzqueda et al., 2020), two in the north of the distribution (Mt Finnigan, Big Tableland) and two in the south (Cardwell Range, Paluma Range). Uzqueda et al. (2020) used modelling to infer widespread declines of *D. m. gracilis* in recent decades, particularly in regards to large habitat patches. They defined six persistent subpopulations, with estimates for these ranging from approximately 8 to 160 individuals, and a total estimate for *D. m. gracilis* of approximately 424 (±110) individuals (Uzqueda et al., 2020). However, they concluded that some of these were likely over-estimates (and hence so too the total estimate), mostly in relation to the likely absence of *D. m. gracilis* from much of the area modelled as currently suitable habitat in the regions of the Atherton Tablelands and Bellenden Ker Range (Uzqueda et al., 2020).

In this study, we conducted detailed camera-trapping surveys across the range of *D. m. gracilis* to: (1) refine population estimates for each subpopulation and (2) assess patterns of distribution against elevation and vegetation type. From these results, we also re-assess the conservation status of *D. m. gracilis* under the EPBC Act.

METHODS

Study area

The study area was the Wet Tropics bioregion of Queensland, encompassing the current range of *D. m. gracilis* from Thornton Peak in the north to the south-eastern region of the Atherton Tablelands, including South Johnstone and Tully River in the south (Uzqueda et al., 2020; Figure 1). The habitat in these primarily upland areas includes rainforest and adjacent high-elevation wet and dry sclerophyll forests, on granite and basalt-derived soils (Burnett, 2001; Figure 1).

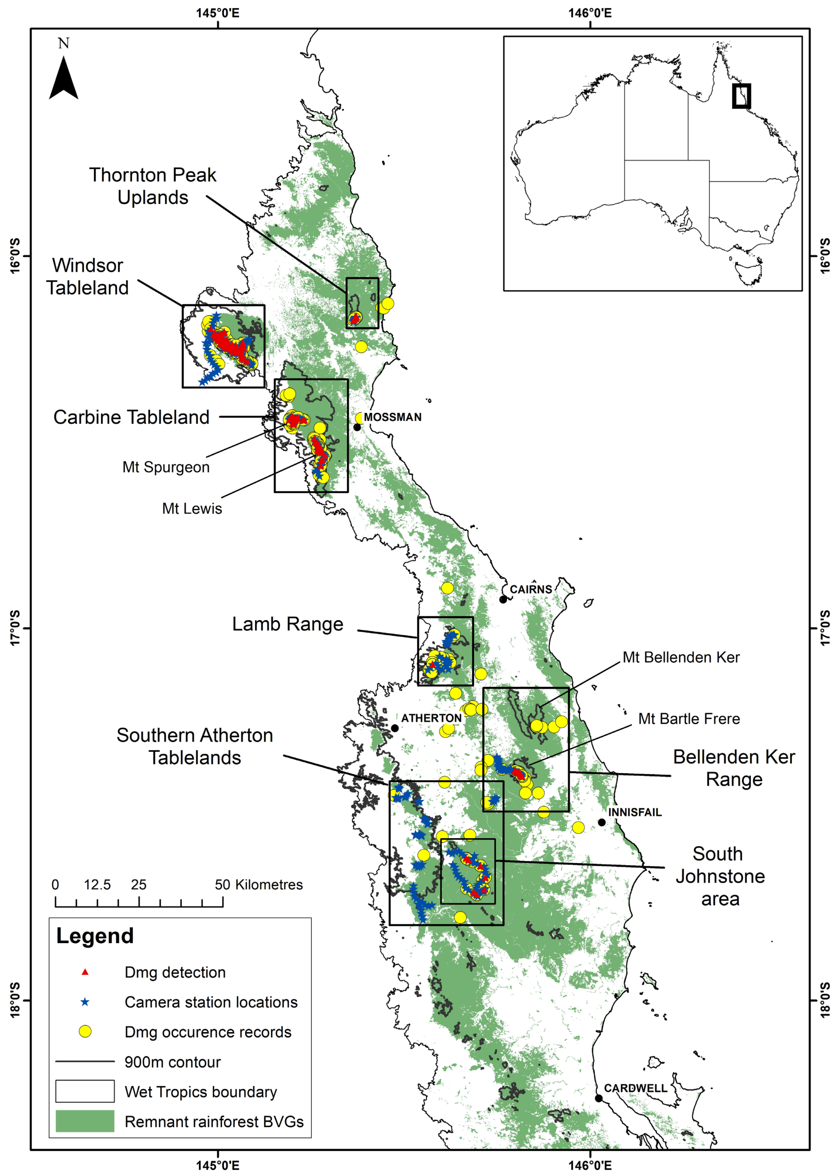

FIGURE 1 Map of the current distribution of northern spotted-tailed quoll in the Wet Tropics bioregion, showing remnant rainforest (as defined by broad vegetation groups (BVGs) (Queensland Herbarium, 2021)), 900 m contour line, and post-2000 *D. m. gracilis* occurrence records. Camera trapping locations in this study (June 2017–May 2019) are shown as blue stars, with red triangles showing cameras which detected *D. m. gracilis*. Boxed areas highlight the core subpopulations.

Quoll surveys

Camera trapping was used to provide an estimate of quoll density within each subpopulation (herein 'population' refers to the total population of animals across their entire distribution, and 'subpopulation' refers to animals in each of the six defined areas within the entire distribution of *D. m. gracilis*). Surveys were undertaken in these six known regions with extant subpopulations of *D. m. gracilis* (Uzqueda et al., 2020): (i) Windsor Tableland, (ii) Carbine Tableland, (iii) Thornton Peak Uplands, (iv) Lamb Range, (v) Bellenden Ker Range, and (vi) the southern/eastern Atherton Tablelands (Figure 1). Camera trapping was undertaken across 341 unique stations, each comprised of a single camera trap and bait set-up, from June 2017 to May 2019 (Table 1). Camera trapping spanned an elevational range of

TABLE 1 Details of all camera trap surveys

Quoll subpopulation	Survey site	Survey period	# camera stations	Trap nights	Bait type	LHS
Thornton Peak Uplands	Thornton Peak	29 Aug–14 Sep 2018	11	172	BC	R
Windsor Tableland	Rainforest	31 May–14 June 2017	20	540	BB	B
		16 Sep–1 Oct 2017	36	403	BC	R
		11–26 Nov 2017	40	458	BC	R
		13–29 Dec 2017	40	415	BC	R
		23 Apr–11 May 2018	79	812	BC	B
		21 June–14 July 2018	19	254	BB	B
		17 Sep–1 Oct 2018	19	258	BB	R
	Wet/dry sclerophyll forest	4–18 Aug 2018	24	351	BC	B
Carbine Tableland	Mt Lewis	5–20 June 2017	24	384	BB	B
		22 June–7 Jul 2018	29	400	BC	B
		8–22 Sep 2018	20	277	BB	R
	Mt Spurgeon	13–29 May 2018	23	195	BC	B
Lamb Range	Danbulla NP	22 June–15 July 2018	15	337	BB	B
	Kahpalim Rock (Dinden NP)	18 April–3 May 2018	12	101	BB	—
Bellenden Ker Range	Mt Bartle Frere	3–22 June 2018	35	530	BC	B
		7–21 Sep 2018	5	56	BB	—
Southern Atherton Tablelands	Towalla Rd	6–21 Sep 2018	5	75	BC	—
	Mt Hypipamee NP	29 April–13 May 2019	3	42	BC	—
	Herberton Range NP	29 April–13 May 2019	4	56	BC	—
	Mt McHugh/ Misty Mountain Nature Refuge	27 April–12 May 2019	5	75	BC	—
	Southern Atherton Tableland Nature Refuges: Cassowary Crossing, Lemuroid Leap, Ringtail Crossing, Dirrans End, Taylor's Hill	27 April–14 May 2019	10	142	BC	—
	Mt Fisher (Malaan NP)	30 April–14 May 2019	5	70	BC	—
	Majors Mountain (Tully Gorge NP)	5–20 Sep 2018	7	105	BC	—
	South Johnstone area (Wooroonooran NP)	9–25 Aug 2018	37	478	BC	B
		4–20 Sep 2018	8	128	BC	B
	Tully Falls NP	26 April–10 May 2019	16	224	BC	—

Note: Bait type refers to bait canister (BC) or bait bag (BB) = bait bag. Surveys where quolls were recorded were assigned to the pertinent life history stage (LHS) of that period: B = breeding (May to August), R = joey rearing (September to December).

500–1570 m above sea level. Camera-trap survey effort and intensity varied among the six regions (i.e. some subpopulations were surveyed more intensively than others) due to logistical constraints, such as accessibility, number of camera traps available, and number of field personnel.

Each survey period was typically a minimum of 2 weeks, during which time, stations were not revisited to replace or replenish bait (Table 1). Camera stations were established in different configurations depending on survey area accessibility. Typically, stations were established along roads and vehicular tracks at spacings of 500 –1000 m apart, and about 10–50 m perpendicular distance into the forest off the road. When vehicular tracks were not used, stations were set on foot at 200 m to 500 m spacings, parallel to a walking trail or unmarked walking route in a line or grid formation through the forest. The closer trap spacings (i.e. 200–500 m) were established due to access and logistical constraints associated with working on foot in steep and densely vegetated habitat (versus the greater spacings used along roads accessible by vehicle). Trap spacing was always ≤1 km, which ensured there were always at least two camera traps per average *D. m. gracilis* home range (Burnett, 2001), as recommended to maximize capture probabilities (Dillon & Kelly, 2007; Nelson et al., 2014). Wherever possible, camera spacing attempted to cover as large an area as possible within the area of potential habitat, to reduce bias in estimates (Foster & Harmsen, 2012).

Due to availability, four camera-trap models were used during the camera surveys (Bushnell Trophy Cam Aggressor, Bestguarder SG-990 V, Reconyx HC550 Hyperfire, ScoutGuard/BolyGuard 562-C). All cameras were programmed to take three still images per trigger, with either a 0 or 1 s gap between trigger events. The differences between camera models were considered minimal for detecting quolls because they are more readily detectable being a medium-sized mammal and because activity time at bait stations is generally 2–10 min (see Rowland et al., 2020a). At each camera station, a single camera was placed on a tree at a height of 10–50 cm above the ground, facing horizontally but with a slight downwards angle towards a bait. Cameras were baited with one or two raw chicken frames, or up to four raw chicken necks. Two bait presentation methods were used: bait housed in a plastic mesh bag (i.e. 'bait bag'), or bait in an open-ended, enclosed PVC cylinder (i.e. 'bait canister') (Rowland et al., 2020a). The bait bag method was used in earlier surveys but was generally superseded by the bait canister method in later surveys (Table 1) due availability as well as the better resolution on individual identification and sex offered by the bait canister method (Rowland et al., 2020a). In all cases, the bait was placed 1.4–3 m from the camera.

Repeat camera-trapping surveys were undertaken at Windsor Tableland (seven surveys) and Mt Lewis (three surveys) because these subpopulations had been monitored previously, have relatively good accessibility, and were considered the largest (Uzqueda et al., 2020). All other sites were surveyed once only, and were generally very challenging sites to access and survey.

Image analysis

Individual quolls were identified from their distinct spot patterns, sexed, and tagged from camera-trap images using the camera-trap software program Camelot (Hendry & Mann, 2018), following the protocols of Rowland et al. (2020a). Similarly, as per Rowland et al. (2020a), we defined a single detection event as any detection of a quoll within 10 min of a previous detection of that same individual. A separate detection event occurred when a different quoll appeared in the 10-minute period or when the same individual was photographed more than 10 min after the previous detection event of that individual.

Estimating density and population size — general approaches

We estimated the density and number of quolls in each subpopulation, and these were summed to provide an overall population estimate for *D. m. gracilis*. Low numbers of individuals and low recapture rates of these individuals precluded our use of capture–recapture modelling methods (e.g. spatially explicit capture–recapture (SECR)) to estimate quoll numbers in any subpopulation. Instead, our approach was to estimate quoll density from our camera-trap data in each subpopulation, and then multiply this by the area of suitable habitat (i.e. mapped and/or modelled habitat, as per Uzqueda et al. (2020) in that subpopulation).

The density of quolls was estimated using a mean maximum distance moved (MMDM) metric (Parmenter et al., 2003), to estimate the effective trapping area (ETA, in km^2) of each survey period. The minimum number of individuals known to be alive (MNKTBA) was then divided by the ETA in each associated survey period to generate a density estimate. The R software package 'secr' was used to calculate the MMDM along with standard errors (Efford, 2017; R Core Team, 2019).

Due to the number of repeat surveys at Windsor Tableland and Mt Lewis (Carbine Tableland), and an expectation that quolls have different spatial behaviours at different times of the year, we calculated separate MMDM values for three distinct life history stages (LHS) using the same R package as above, by grouping the 2017–2018 surveys at these subpopulations into: breeding season (May–August surveys), joey rearing and juvenile independence (September–December surveys), and dispersal period (January–April surveys) (Burnett, 2001) (Table 1). Whilst MMDM is influenced by factors, such as individual movements (including differences in male versus female movements), season, and bait longevity, we tried to reduce this variation by calculating an MMDM for surveys within distinct LHSs (Foster & Harmsen, 2012). The April 2018 survey at Windsor Tableland was grouped into the breeding season LHS because the survey period extended further into May than April (Table 1). Standard errors (SE) for each MMDM value were converted to 95% confidence intervals to obtain the upper and lower MMDM bounds for each LHS, which was then applied to derive confidence intervals for density estimates and populations sizes. The conversion was achieved by multiplying the SE value with the critical value (5%) from the *t*-distribution matching the degrees of freedom (i.e. sample size −1).

Because of the broad elevational range of surveys and the relatively high number of quoll detections at Windsor Tableland and Carbine Tableland, it was possible to assess whether there was a marked difference in density of *D. m. gracilis* across elevational bands. Densities were estimated within each 100 m elevation band for the surveys at these two subpopulations which detected the highest number individuals (i.e. April 2018 survey at Windsor Tableland; June 2017 survey at Mt Lewis). These densities were then visualized to assess the elevational thresholds at which density changed by an order of magnitude. For Windsor Tableland, densities were an order of magnitude higher above 1000 m than below it, and for Carbine Tableland, this density difference occurred above 1100 m (Appendix S1). The population size estimates for Windsor Tableland and Carbine Tableland were then refined based on estimating density (and population size) separately above and below these elevational thresholds.

Estimating the size of the Windsor Tableland subpopulation

We calculated the extent (km^2) of moderate to high suitability habitat for *D. m. gracilis* by overlaying the 50% threshold species distribution model from Uzqueda et al. (2020) (referred to herein as the '50% threshold SDM area'). The 50% threshold SDM area covered both rainforest and wet sclerophyll areas, and to calculate the SDM areas for each habitat type, we used ArcMap (v10.6.1) (ESRI, 2018) and the broad vegetation group layer (1:1000,000 scale, Queensland Herbarium, 2021). The rainforest 50% threshold SDM area was then further divided into two separate areas (above and below 1000 m) by clipping to the 1000 m contour layer

(Department of Resources, 2021). ETAs were generated for the two elevational areas for each survey by using the respective LHS MMDM value as a buffer distance around each camera station, then totalling the area of the overlapping buffer distances (Appendix S1). Overlapping areas on either side of the contour line were included in the ETAs. To derive the MNKTBA for each elevation zone, numbers of individual quolls were totalled separately across stations where they occurred above 1000 m and below 1000 m. A density was then generated for these two areas for each survey by dividing the MNKTBA by the respective ETA.

All wet sclerophyll habitat was above the 1000 m contour line at Windsor Tableland. Data from the August 2018 survey was used to generate a density estimate for the wet sclerophyll 50% threshold SDM area. To do this, the ETA was derived by totalling the area of overlapping MMDM buffer distances around the camera stations using the breeding season MMDM for Windsor Tableland (Table 1; Appendix S1). Since sclerophyll habitats are generally considered marginal for *D. m. gracilis* (Burnett, 2001), stations located more than two times the MMDM length away from the edge of mapped wet sclerophyll habitat (i.e. in dry sclerophyll habitat) were excluded from the ETA. This is because *D. m. gracilis* is unlikely to traverse further than this distance through these marginal habitat types (Burnett, 2001).

For each survey, estimated population sizes for rainforest habitat above and below 1000 m were each calculated by multiplying the densities by their respective 50% threshold SDM area. Population size was also individually calculated for the wet sclerophyll habitat, by multiplying the density estimate by the wet sclerophyll 50% threshold SDM area. To generate total population size estimates for Windsor Tableland for each of the seven surveys, we combined estimated sizes from rainforest above and below 1000 m for each survey, and the wet sclerophyll habitat estimate. The overall population size estimate was derived by calculating a median of the totals for the seven survey estimates.

Estimating the size of the Carbine Tableland subpopulation

For Carbine Tableland (i.e. Mt Lewis and Mt Spurgeon surveys), we followed the same methodologies as outlined above for Windsor Tableland (i.e. calculating separate densities for rainforest and wet sclerophyll areas, as well as calculating the ETA and MNKTBA estimates). The only difference was that the Windsor Tableland wet sclerophyll density estimate was used for the Carbine Tableland wet sclerophyll 50% threshold SDM area, due to a lack of targeted survey data in this habitat at Carbine Tableland. We assumed similar densities in wet sclerophyll habitat for these two subpopulations due to similar elevations and close geographical proximity (Figure 1).

All camera stations were above 1100 m at Mt Spurgeon; therefore, the density was multiplied by the 50% threshold SDM rainforest area above 1100 m to calculate estimated population size for this survey. The three repeat surveys at Mt Lewis and the single survey at Mt Spurgeon were used to generate three total subpopulation size estimates for the Carbine Tableland. For each of the June 2017 and September 2018 surveys at Mt Lewis, the estimates from above and below 1100 m, and the single wet sclerophyll habitat estimate were totalled. The June 2018 Mt Lewis survey estimate was calculated by first deriving the median between the above 1100 m estimate and the Mt Spurgeon (May 2018) estimate, as they were both within the breeding season LHS, then adding the below 1100 m estimate from Mt Lewis and single wet sclerophyll habitat estimate. A median of the totals from these three estimates was calculated to derive an overall subpopulation size estimate for Carbine Tableland.

Estimating sizes of the remaining four subpopulations

Ideally, a separate MMDM value would have been estimated for each survey period; however, the requirement for numerous spatial recaptures precluded this. Instead, due to the higher number of repeat surveys at Windsor Tableland (Table 1) and thus the more detailed movement data, the MMDM LHS estimates from this subpopulation were used to define the ETAs for all other subpopulations (Thornton Peak, Lamb Range, Mt Bartle Frere, and South Johnstone) based on their survey periods (Table 1). Density estimates for these subpopulations were otherwise derived using the methodologies described above.

The suitable habitat area for the Thornton Peak Uplands and Lamb Range were both defined as the mapped rainforest above the 900 m contour line. In both cases, this included much of the 50% threshold SDM area and clipping at 900 m elevation was performed to remove areas of the 50% threshold SDM area that are non-rainforest and have no evidence of historic or current quoll occupancy (Uzqueda et al., 2020).

The suitable habitat area for Mt Bartle Frere and Mt Bellenden Ker was also defined as the 50% threshold SDM area clipped to the 900 m contour line but the decision for this was less clear-cut. Our survey effort covered a wide elevational range, from roughly 650 m to >1500 m near the summit of Mt Bartle Frere. We decided to be conservative and use 900 m because our survey effort was restricted to the western side of Mt Bartle Frere and may not be reflective of the entire Bellenden Ker Range. The Bellenden Ker Range also includes Mt Bellenden Ker, which has recent *D. m. gracilis* records (Uzqueda et al., 2020), although it was not surveyed in this study. The Mt Bartle Frere density estimate was extrapolated to above 900 m at Mt Bellenden Ker to estimate subpopulation size. These two mountaintops were considered to have similar densities due their close geographical proximity, and similar elevational range and vegetation (Figure 1).

We conducted camera-trapping surveys in the southern and eastern Atherton Tablelands, which included the South Johnstone area due to records in the last decades (Uzqueda et al., 2020; Figure 1). Because the surveys only revealed *D. m. gracilis* in the South Johnstone area, we clipped the 50% threshold SDM area to exclude other parts with no recent records (i.e. north of the Palmerston Highway, and the following areas of the southern Atherton Tablelands region: Mt Fisher, Majors Mountain area, Tully Falls National Park (NP) and the area of Koombooloomba NP south of Tully Gorge; Figure 1). To derive the MNKTBA for the southern/eastern Atherton Tablelands subpopulation, we used the total number of individual quolls detected across stations for both surveys in 2018, plus an additional *D. m. gracilis* individual known to be present at the time (detected during a parallel genetic study by one of us: CH). We then applied this density to the South Johnstone 50% threshold SDM area, which encompassed the continuous rainforest habitat surveyed in 2018 and also included the adjacent high-elevation areas (i.e. >700 m elevation) in the Walter Hill Range and Japoon NP.

Elevation and vegetation associations

Detection rates of quolls (determined by dividing the number of detection events by the number of camera-trap nights during a survey period) were assessed against elevational data, particularly for repeat surveys conducted at Windsor Tableland and Mt Lewis. A key objective was to compare the detection rates of males and females with elevation. Detection rates of all individuals and of sexed males and females were summarized for each subpopulation in 100 m elevational bands.

To assess *D. m. gracilis* occurrence against vegetation types (or Regional Ecosystems; REs) across the study area, records of *D. m. gracilis* sourced from Uzqueda et al. (2020) and this study were intersected with the RE (Queensland Herbarium, 2021) layer using ArcMap (ESRI, 2018). These records were then summarized by vegetation type, with a focus on detection rate (i.e. number of detection events divided by the number of total camera-trap nights across all survey periods within each RE, as a measure of quoll activity).

RESULTS

Dasyurus m. gracilis was detected at 122 of the 341 camera stations. Across all surveys, we obtained 937 detection events, of 117 distinct individuals, during 8907 trap-nights. Individuals were able to be identified from 99.5% of detection events. Sex was able to be resolved for 53% of these individuals, primarily from camera-trap images using the bait canister method at camera stations (outlined in Rowland et al., 2020a).

Density and abundance across the six subpopulations

We estimated a total population size of approximately 221 (128–461) *D. m. gracilis* in October 2018 (Table 2). These were distributed in six subpopulations (Figure 1), ranging in size from the largest subpopulation in the north at Carbine Tableland (approximately 105 individuals), to the smallest at Lamb Range in the south (approximately six individuals) (Table 2).

The Carbine Tableland is estimated to have the largest subpopulation of *D. m. gracilis*, with approximately 105 (47–256) individuals, as of October

TABLE 2 Density estimates and population sizes from each of the *D. m. gracilis* subpopulations

Subpopulation	Total habitat area (km^2)	*N*	Uzqueda et al.	Comparison
Windsor Tableland	88.9 (>1000 m); 30.6 (<1000 m); 30.3 (wet sclerophyll)	37 (27.8–61.1)	33.8 ± 9.2	≈
Carbine Tableland	135.4 (>1100 m); 120.2 (<1100 m); 30.5 (wet sclerophyll)	105 (46.5–256.4)	127.9 ± 29.1	≈
Thornton Peak Uplands	17.05	16 (9.9–28.7)	7.9 ± 2.2	>
Lamb Range	58	6 (3.8–10.3)	10.4 ± 2.8	≈
Bellenden Ker Range (total)		32 (20.6–60.8)	82.0 ± 22.4	<
Mt Bartle Frere	34.87	13 (8.3–24.6)	N/A	N/A
Mt Bellenden Ker	51.4	19 (12.3–36.2)	N/A	N/A
South Johnstone/Atherton Tablelands	214.2	26 (19.0–44.1)	159.6 ± 43.5	<
Mt Finnigan	0.61	0	0.1 ± 0.04	N/A
Cardwell Range	10.75	0	2.4 ± 0.7	N/A
Total population		221 (128–461)	424.1 ± 110	<

Note: *N* is the total number of individuals estimated for each population, and overall, along with the 95% confidence intervals in brackets. The 'Comparison' column compares these results with recent estimates by Uzqueda et al. (2020): ≈ represents a similar estimate (i.e. within the standard error of Uzqueda et al. (2020)); > represents a higher estimate; < represents a lower estimate. We did not conduct estimates for Mt Finnigan and Cardwell Range.

2018 (Table 2). As for Windsor Tableland, density estimates varied across repeat surveys at Carbine Tableland, where the June 2018 survey at Mt Lewis had the lowest estimated total number of quolls (74 (47–135) individuals) and the June 2017 survey had the highest number of individuals, estimated at approximately 132 (82–256) quolls. Densities at Mt Lewis were consistently higher above 1100 m (mean estimate across surveys (SE) = 0.51 (0.14) individuals per 1 km^2; max estimate = 0.75), compared with below it (mean estimate = 0.22 (0.05) individuals per 1 km^2; max estimate = 0.3) (Appendix S1).

Compared with other subpopulations, Windsor Tableland was estimated to have a moderate-sized subpopulation of approximately 37 (28–61) individuals, as of October 2018 (Table 2). Population estimates at Windsor Tableland were however highly variable across repeat surveys between June 2017 and October 2018, ranging from an estimated population size of 8 (6–14) to 40 (29–70) individuals. Densities in the rainforest were substantially higher above 1000 m (mean estimate across repeat surveys (SE) = 0.35 (0.05) individuals per 1 km^2; max estimate = 0.45) than below 1000 m (mean estimate = 0.05 (0.03) individuals per 1 km^2; max estimate = 0.17) (Appendix S1). The single density derived from the wet sclerophyll forest (August 2018 survey) was very low: mean = 0.02 individuals per 1 km^2 (Appendix S1).

The single survey at Thornton Peak was the highest density of all estimates in this study (0.91 (0.58–1.68) individuals per 1 km^2) (Appendix S1). Despite this density, the relatively small estimated area of suitable habitat resulted in a small population size estimate (approximately 16 (10–29) individuals) for the Thornton Peak Uplands subpopulation (Table 2).

Bellenden Ker Range had an estimated density of 0.37 (0.24–0.7) individuals per 1 km^2, based on the June 2018 survey at Mt Bartle Frere (Appendix S1). This gave an estimated subpopulation size of 13 (8.3–24.6) individuals for Mt Bartle Frere, and 19 (12.3–36.2) individuals for Mt Bellenden Ker. Therefore, the Bellenden Ker Range subpopulation is estimated to be approximately 32 (20.6–60.8) individuals (Table 2).

In the southern and eastern Atherton Tablelands, quolls were only detected in the South Johnstone area, with a relatively low density of 0.12 (0.09–0.21) individuals per 1 km^2; thus producing a moderate population size estimate of 26 (19–44) individuals (Table 2; Appendix S1).

The single survey at Lamb Range revealed only three individuals on the cameras, at a low-density estimate of 0.1 (0.07–0.18) individuals per 1 km^2 (Appendix S1), and a very small subpopulation estimate of approximately 6 (4–10) individuals (Table 2).

Elevation

In general, detection rates were considerably greater at higher elevations (Figure 2). Of all detection events, 78.6% were above 1100 m, including 87.8% of female and 70.1% of male detections (Figure 2). No females were identified below 1100 m elevation, apart from in the South Johnstone area. South Johnstone was the only area where multiple individuals were detected below 900 m elevation, with a population of males and females present between 600 and 900 m elevation (Figure 2).

Elevational ranges were assessed with more rigour at Windsor Tableland and Mt Lewis due to the repeat surveys. These two areas show broadly the same pattern of detections by elevation (Figure 2). In both areas, the lowest camera-trapping effort was in the 900–1000 m band, where there were relatively few detections in both areas. Detection rates were higher above 1000 m in both areas and all identified females were above this elevation.

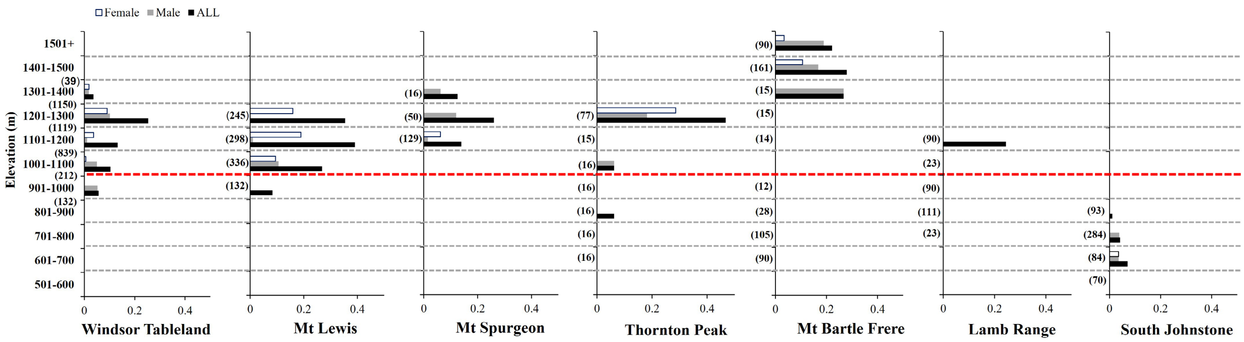

FIGURE 2 Quoll detection rates from camera trapping surveys and known male and female individuals across 100 m elevational bands at all sites. Numbers in brackets show the survey effort (total camera trap nights) within each elevational band. Dashed red line indicates the 1000 m elevation. For Windsor Tableland and Mt Lewis, average detection rate (detection rate is the number of detection events divided by the number of camera trap nights during a survey period) was calculated from repeat surveys. For South Johnstone, detection rates represent combined data from August and September 2018 surveys.

The average detection rate at Windsor Tableland for stations above 1000 m was 0.17 (0.05), versus 0.03 (0.02) at stations below 1000 m. Surveys at Mt Lewis revealed an average detection rate above 1100 m of 0.39 (0.16), versus 0.18 (0.08) at stations below 1100 m. These patterns were particularly evident for females (Figure 2). At Windsor Tableland, the average detection rate of females was 0.05 (0.01) above 1000 m and no females were detected below 1000 m, and the corresponding rates for Mt Lewis above and below 1100 m were 13.9 (11.2) and 7.5 (6.7), respectively. There was no particular pattern evident for male detections (Figure 2).

Vegetation associations

All records of *D. m. gracilis* occurred in a total of 19 Regional Ecosystems (Appendix S2). The REs with the highest detection rates and numbers of individuals detected (including both males and females) were 7.12.16a (0.16, 80), 7.12.19a (0.21, 38), and 7.12.20 (0.27, 13). The highest detection rate (0.42) came from one camera station in RE 7.12.9, capturing a total of five individuals. With the exception of 7.12.9, these REs are all types of 'simple vine forest' in the wet rainfall zones (Queensland Herbarium, 2021) (Appendix S2). Detection rates in wet sclerophyll habitat (i.e. 7.12.21a, 7.12.22a) at Windsor Tableland were very low (<0.03).

DISCUSSION

Current distribution

Obtaining accurate estimates of distribution and population density of elusive marsupial predators is essential to detect declines and guide management actions. In this study, camera-trapping surveys detected *D. m. gracilis* in all six extant subpopulations identified by Uzqueda et al. (2020): Thornton Peak Uplands, Windsor Tableland, Carbine Tableland, Lamb Range, Bellenden Ker Range, and the South Johnstone area of the south-eastern Atherton Tablelands. Importantly, our results confirmed the continued presence of *D. m. gracilis* at Thornton Peak; the resolution of which was a key recommendation of Uzqueda et al. (2020). The findings support the conclusion that *D. m. gracilis* is now likely absent from the vast majority of its former range on the Atherton Tablelands, providing further evidence of a severe decline in recent decades from what was historically the largest habitat area, and presumably, subpopulation (Burnett, 2001; Uzqueda et al., 2020).

Estimates of density and size of the six subpopulations

We estimated that Carbine Tableland had a relatively high density of *D. m. gracilis*, particularly above 1100 m, and represents the largest subpopulation of the subspecies (median = 105, range = 47–256; Table 2). Our estimate was similar to that of Uzqueda et al. (2020) (127.9 (±29.1) individuals). While we note the variations across our three repeat temporal estimates (132 (82–256) individuals in June 2017, 74 (47–135) individuals in June 2018, and 105 (46–1298) individuals in September 2018), this variation may be explained by differences in movement patterns, and hence detection, across different seasons rather than rapid changes in actual population size.

Our Windsor Tableland subpopulation estimate of 37 (28–61) individuals was also similar to the estimate reported by Uzqueda et al. (2020) (34 (±9.2) individuals). The methods for calculating density differ between these two studies and hence the similarity in results provides confidence in the estimates, and that our estimate herein was based on many repeat surveys. Further support for our estimate is demonstrated by the highest number of individual quolls being 24, recorded during the April 2018 survey where camera stations covered a substantial proportion of the suitable habitat area at Windsor Tableland.

For the Thornton Peak Uplands, we surveyed in the highest section at Thornton Peak, finding high density and producing an estimate of approximately 16 (10–29) individuals. This is a higher estimate than that provided by Uzqueda et al. (2020), but is likely more accurate due to the fact that we surveyed Thornton Peak to obtain a local density estimate, whereas they extrapolated a density estimate from Windsor Tableland. The key question remaining for this subpopulation is whether *D. m. gracilis* also occurs in the upland areas (i.e. above 900 m elevation) immediately north-east of Thornton Peak, in which case the subpopulation could be larger.

The three subpopulations in the central/southern Wet Tropics are all estimated to be small (Table 2). Our estimate of the Bellenden Ker Range subpopulation of 32 (21–61) individuals was much lower than the estimate of 82 (±22.4) by Uzqueda et al. (2020). The main differences are that our estimate involved a local density estimate (versus an estimate from Windsor Tableland in Uzqueda et al. (2020)), and we refined the area of occupancy to above 900 m elevation. The SDM produced by Uzqueda et al. (2020) predicted suitable habitat in mid-elevation and lowland areas on the eastern side of the Bellenden Ker Range and, as acknowledged by the authors, these areas are unlikely to be suitable habitat (and have very few records). Of note, is that we recorded no quolls below 1100 m elevation on the Bellenden Ker Range, despite surveying down to 680 m elevation (Figure 2). Therefore, our estimate of approximately 32 individuals (based on a 900 m lower elevational limit) may be conservative and we caution that the size of the Bellenden Ker Range subpopulation may be smaller.

The Atherton Tablelands region contains the greatest number of historic records, the greatest area of modelled habitat, and the largest recent subpopulation size estimate of approximately 160 (±43.5) individuals (Uzqueda et al., 2020). However, the authors of that study suggested that quolls may no longer be in much of that modelled habitat due to recent declines. Indeed, our camera-trapping surveys over extensive areas of this modelled habitat, which historically had many records, yielded no detections except in the South Johnstone area (Figure 1). This conforms to occurrence records over the last 5 years, nearly all of which are derived from the South Johnstone area. Based on our surveys in this locality, we estimated that the population in the South Johnstone area is approximately 26 (19.0–44.1) individuals, and we believe this may be the only remaining population on the Atherton Tablelands.

Our results suggested a very low density of quolls at Lamb Range, and an estimate of just six individuals (4–10). The subpopulation at Lamb Range was previously estimated at approximately 10 (±2.8) individuals, although likely lower due to a recent observed decline (Uzqueda et al., 2020). These results suggest this subpopulation is persisting at critically low numbers.

Total population size and conservation status

The subpopulation estimates summed together suggest that the total population of *D. m. gracilis*, as of October 2018, was approximately 221 (128–461) individuals. This total is considerably lower than the population estimate of 550 individuals, as of 1993 (Burnett, 2001), and the recent estimated total of 424 (±110) by Uzqueda et al. (2020). However, it is not possible to infer a decline from these numbers because the methodologies differed across all three studies. The main difference is that the density estimates used in the previous studies were, broadly speaking, extrapolated across the distribution of *D. m. gracilis* from high-density subpopulations (i.e. Windsor and Carbine Tablelands). In contrast, the approach used here is more accurate in using density estimates from each subpopulation based on the survey data. Thus, as acknowledged by Burnett (2001) and Uzqueda et al. (2020), previous estimates were likely inflated due to extrapolating high densities to areas of suitable habitat where densities were lower or where *D. m. gracilis* was likely absent (e.g. central and southern Atherton Tableland region and lower elevation areas of the Bellenden Ker Range). Methodologies and fine-scale distribution have been refined across all three studies, and this study used systematic camera-trapping data and density estimates for each subpopulation, so we have confidence that the current population is in the vicinity of our estimate rather than the two previous estimates.

The current key threats to *D. m. gracilis* are not well-resolved, and are believed to include poisoning from ingesting cane toads, competition with introduced predators (e.g. feral cats (*Felis catus*)), and climate change (Burnett & Marsh, 2004; Uzqueda et al., 2020). Direct control of invasive species, such as hand-removing *R. marina* along roads at Windsor Tableland, Carbine Tableland and Lamb Range (Uzqueda et al., 2020) will likely benefit the subspecies. The Bellenden Ker Range subpopulation is estimated herein to be small and is known to co-occur with an apparently high density of *F. catus* (Rowland et al., 2020b). These may be a direct threat to *D. m. gracilis* through competition and potential disease transfer (Burnett & Marsh, 2004). Therefore, every effort should be made to reduce *F. catus* numbers on Mt Bartle Frere and Mt Bellenden Ker. Due to predicted climate change impacts (Williams et al., 2012), subpopulations with large areas of adjacent dry and wet sclerophyll forest (Windsor Tableland, Carbine Tableland, Lamb Range) may become seriously threatened by severe wildfire events. Fire intensity can become sufficient to burn from wet sclerophyll forests into rainforest that has not burnt in recorded history (e.g. as seen at Eungella NP and further south; Hines et al., 2020). Extreme weather events (i.e. extended droughts) could provide catastrophic conditions for wildfire in these habitat types, which could potentially severely impact *D. m. gracilis* subpopulations in adjacent rainforest.

Dasyurus m. gracilis is currently listed as Endangered under the EPBC Act (Department of the Environment, 2021); however, our results suggest that this should be revised to Critically Endangered. This is based on Criterion C: <250 individuals; C2, an observed, estimated, projected or inferred continuing decline; and its geographic distribution is precarious for its survival based on (a) number of mature individuals in each subpopulation <50 (Threatened Species Scientific Committee, 2018). Although our subpopulation estimate for Carbine Tableland is greater than 50 individuals, our estimates for the remaining subpopulations are all substantially less than 50 and the average of all six subpopulation estimates is 37 individuals.

Elevation as a determinant of distribution and density

This study confirms that *D. m. gracilis* is most abundant at high elevations. The majority of detections (and higher densities) came from the higher elevations surveyed in each subpopulation area. In particular, we discovered that densities were relatively higher above 1000 m and 1100 m asl, respectively, for the subpopulations of Windsor Tableland and Carbine Tableland. Interestingly, this seems strongly the case for females, with nearly 90% of female detections coming from above 1100 m across all subpopulations. The pattern was still evident for males, with 70% of detections above 1100 m (Figure 2). Previous studies have suggested that the important threshold is approximately 900 m elevation across the range (Burnett, 2001), or at least for some subpopulations (Uzqueda et al., 2020), but our findings indicate that *D. m. gracilis* is generally more restricted in elevational range. This result suggests an elevational range higher than most other endemic Wet Tropics species, including several ringtail possum species (de la Fuente & Williams, 2022), as well as other taxa, such as birds (Williams & de la Fuente, 2021), frogs (Hoskin & Higgie, 2005), and ants (Leahy et al., 2020).

Our results pose the obvious question of why *D. m. gracilis* is generally restricted to the highest elevations. Climatic conditions associated with the mountaintops (high rainfall, low temperatures, and low seasonality) were the primary predictors of habitat suitability in the modelling of Uzqueda et al. (2020). A potential driver of this may be a preference for, or restriction to, cool temperatures of the uplands (i.e. physiological restriction), as suggested for some co-occurring upland vertebrates (Moritz et al., 2005, 2012). It may also reflect restriction to areas of high productivity (i.e. relatively high prey diversity and/or density). The subspecies primarily feeds on small to medium-sized mammals (Burnett, 2001), which are higher in diversity and abundance in the uplands of the Wet Tropics (Rowland et al., 2020b; Williams, 1997; Williams et al., 2010). Upland restriction may also be determined by the distribution of identified threats, which are generally associated with human activities and hence decrease with rainforest patch size and distance to the edge (Burnett & Marsh, 2004; Uzqueda et al., 2020). In the Wet Tropics, human activity is greatest in the lowlands and flat areas, and most protected reserves are located in the upland regions, with the remotest areas being the large upland areas of the northern Wet Tropics (Department of Environment & Science, 2019). Distance from threats may therefore contribute to high-elevation restriction in the Wet Tropics (Uzqueda et al., 2020).

The one exception to the high-elevation result is the persistent subpopulation in the South Johnstone area, detected only at 600–800 m elevation (Figure 2). The survival of an unusually 'lower' elevation subpopulation at South Johnstone probably reflects local climate, fertility, and remoteness from threats. The South Johnstone area has high annual rainfall and is fertile (due to relatively 'recent' basaltic flows from the Atherton Tablelands), therefore, it may support high mammal prey diversity and abundance (see Rowland et al., 2020b) compared with many other mid-elevation areas of the Wet Tropics (Burnett, 2001).

Vegetation type as a determinant of distribution and density

Occurrence records and camera-trap records of *D. m. gracilis* primarily come from three upland rainforest vegetation types (Appendix S2). This is similar to the findings of Burnett (2001), and likely relates to the high-elevation conditions and associated prey activity patterns (authors, unpublished data, 2017–2019), rather than rainforest type per se. Wet sclerophyll forest is the other broad habitat type with extensive distribution in the uplands of the Wet Tropics (Stanton et al., 2014). Camera trapping through the wet sclerophyll forest at Windsor Tableland revealed a very low detection rate (0.02), compared with relatively high numbers of individuals and detection rates in the adjacent upland rainforest during a similar period (Appendix S2). There are several *D. m. gracilis* occurrence records from wet sclerophyll forest, although our results suggest that these individuals are transients rather than resident populations in this habitat type.

Recommendations

For future population estimates, higher numbers of camera stations (i.e. >50), set across extensive grids through the forest (rather than linear transects), would likely generate larger sample sizes and higher recapture rates, which would enable the use of more accurate methods for density estimation, such as SECR (Forsyth et al., 2019; Foster & Harmsen, 2012; Rovero et al., 2013). However, logistical difficulties associated with the rugged terrain at most sites would need to be taken into consideration. Our results may have been influenced by the different camera-trap arrays used between and within subpopulations, because trap spacing and arrays may have influenced the numbers of quolls visiting the stations. Similarly, surveys in different seasons may have also influenced the results as movement patterns, especially for males, can vary greatly between breeding and non-breeding seasons (Burnett, 2001). One of the bait station methods for camera-trap surveys used in this study enables the sexing of individuals from images (Rowland et al., 2020a); however, we did not use it for all surveys due to logistical and budget constraints. Ideally, a single camera station method would be used in future surveys and monitoring. Additionally, the same camera-trap model (and program settings) should be used for future surveys and monitoring due to differences in sensitivity, detection zones, and trigger speeds between different camera models (e.g. Meek et al., 2014).

Future surveys should aim to estimate population size using the number of individual males and females, and in different seasons, to account for differences in home range radius between the sexes, thus generating more reliable density estimates (Foster & Harmsen, 2012). Continued annual monitoring using standardized camera-trapping methodologies (e.g. Rowland et al., 2020a) should be undertaken at Windsor Tableland, Carbine Tableland, Lamb Range (particularly regarding extremely low numbers), and South Johnstone. Surveys in the latter area should also extend to adjacent high-elevation habitat of the Walter Hill Range and uplands on the northern side of Tully Gorge, to better resolve the distribution and size of this subpopulation. We recommended that monitoring of the more remote and/or less accessible subpopulations in the Thornton Peak Uplands (including adjacent upland areas) and Bellenden Ker Range occur every 3 years.

Monitoring of the subpopulations will be critical to correlate population trends with monitoring of threats, such as the abundance of cane toads (*R. marina*) and feral cats (*F. catus*), and monitoring of mammalian prey abundance (e.g. using data derived from camera-trapping surveys) as a proxy of climate change impacts (Hoffmann et al., 2019; Uzqueda et al., 2020; de la Fuente & Williams, 2022). We also recommend that land managers ensure burning regimes in the wet and dry sclerophyll forests of the Wet Tropics are undertaken with suitable frequency and intensity to protect the core rainforest areas from wildfires, particularly at Windsor Tableland and Carbine Tableland.

AUTHOR CONTRIBUTIONS

Jesse Rowland: Conceptualization (equal); formal analysis (lead); methodology (equal); resources (lead); writing – original draft (lead); writing – review and editing (lead). **Conrad Jules Hoskin:** Conceptualization (supporting); formal analysis (supporting); methodology (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Scott Burnett:** Conceptualization (equal); formal analysis (supporting); methodology (equal); writing – review and editing (supporting).

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CONFLICT OF INTEREST

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article

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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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