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RESEARCH ARTICLE

Resource manipulation reveals interactive phenotype-dependent foraging in free-ranging lizards

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Abstract

1. Recent evidence suggests that individuals differ in foraging tactics and this variation is often linked to an individual's behavioural type (BT). Yet, while foraging typically comprises a series of search and handling steps, empirical investigations have rarely considered BT-dependent effects across multiple stages of the foraging process, particularly in natural settings.
2. In our long-term sleepy lizard (*Tiliqua rugosa*) study system, individuals exhibit behavioural consistency in boldness (measured as an individual's willingness to approach a novel food item in the presence of a threat) and aggressiveness (measured as an individual's response to an 'attack' by a conspecific dummy). These BTs are only weakly correlated and have previously been shown to have interactive effects on lizard space use and movement, suggesting that they could also affect lizard foraging performance, particularly in their search behaviour for food.
3. To investigate how lizards' BTs affect their foraging process in the wild, we supplemented food in 123 patches across a 120-ha study site with three food abundance treatments (high, low and no-food controls). Patches were replenished twice a week over the species' entire spring activity season and feeding behaviours were quantified with camera traps at these patches. We tracked lizards using GPS to determine their home range (HR) size and repeatedly assayed their aggressiveness and boldness in designated assays.
4. We hypothesised that bolder lizards would be more efficient foragers while aggressive ones would be less attentive to the quality of foraging patches. We found an interactive BT effect on overall foraging performance. Individuals that were both bold and aggressive ate the highest number of food items from the foraging

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array. Further dissection of the foraging process showed that aggressive lizards in general ate the fewest food items in part because they visited foraging patches less regularly, and because they discriminated less between high and low-quality patches when revisiting them. Bolder lizards, in contrast, ate more tomatoes because they visited foraging patches more regularly, and ate a higher proportion of the available tomatoes at patches during visits.

5. Our study demonstrates that BTs can interact to affect different search and handling components of the foraging process, leading to within-population variation in foraging success. Given that individual differences in foraging and movement will influence social and ecological interactions, our results highlight the potential role of BT's in shaping individual fitness strategies and population dynamics.

KEYWORDS

animal personality, behavioural consistency, exploration–exploitation trade-off, food availability, foraging behaviour, home range size, intraspecific variation, movement ecology

1 | INTRODUCTION

Foraging for food is one of the main tasks animals face during their lives, with major consequences for individual fitness and population/community dynamics (Stephens et al., 2007). Accumulating evidence suggests that individuals differ consistently in their foraging tactics and that this variation is associated with individual differences in morphology or physiology (Oudman et al., 2016; Pires & Melo, 2020). Recent work also suggests that among-individual differences in foraging tactics can be linked to an individual's behavioural type (BT), that is consistent (across time or context) among-individual differences in behavioural traits (Ersoy et al., 2022; Fülöp et al., 2019; Milligan et al., 2017; Sih et al., 2004).

Boldness (often measured as an individual's tendency to take risks or respond to novelty) and aggressiveness have been independently linked to various aspects of foraging, including search behaviour (Patrick et al., 2017; Traisnel & Pichegru, 2019), resource exploitation (Theódórsson & Ólafsdóttir, 2022), foraging efficiency (DiRienzo et al., 2020; Tan et al., 2018) and foraging site fidelity (Harris et al., 2020). Given that animals often face a trade-off between safety and resource acquisition, boldness is regularly connected to how individuals forage, particularly under predation risk (Dammhahn & Almeling, 2012; Eccard et al., 2020). For example, bolder jumping spiders are consistently more active foragers than shy spiders across different landscapes of risk (Steinhoff et al., 2020). On the contrary, the relationship between aggressiveness and foraging is less clear. Aggressive individuals can monopolise food resources by competitively excluding others (Pintor et al., 2009), but they may also forgo foraging opportunities when defending or maintaining territories (Ord, 2021). In general, however, studies investigating BT-dependent effects on foraging have focused on one component at a time in the overall foraging process (e.g. foraging rate or foraging search patterns), whereas foraging typically comprises a series of successive search and handling steps (Stephens et al., 2007). To understand how BTs affect individual foraging tactics, we need to explore their effects on a more complete set of steps of the foraging process—from how individuals search for food, to how they handle food once they find it. Empirical studies on the effects of BTs on different steps of the foraging process remain underexplored, particularly in natural settings where foraging behaviour is also mediated by several environmental factors (e.g. variation in habitat characteristics, predation risk or social dynamics).

The total amount of food an individual consumes can be conceptualised as resulting from interactions among several components (Figure 1). At the first level (*i* in Figure 1), for active foragers, encounter rates with food should often depend on the individual's home range (HR) size. Animals with larger HRs might often encounter more food because larger areas may contain more resources. Countering this, however, is the possibility that higher food density may cause animals to have a smaller HR size (Börger et al., 2008). Home range size and search behaviour, in turn, can together affect consumption through (*ii*) the number of unique patches a forager visits and (*iii*) the number of patch revisitations. These two components then together determine the (*iv*) total number of visits to food patches. HR size might also affect (*v*) the time until patch discovery, because in larger HRs it might take longer to arrive at peripheral sites. In many species where access to resources is not exclusive to a single individual, finding food patches more slowly may result in less available resources upon arrival to already-depleted patches. Thus, the time until patch discovery (or revisitation if patches are renewable), could also influence the number of food items consumed at a foraging patch. The product of total patches visited, and the amount of average food eaten per patch visit (*vii*) will determine an individual's overall resource consumption.

In principle, among-individual variation in any one (or more) of these seven components of the foraging process (HR can be viewed as a mediator, rather than an actual component) may result in overall differences in resource consumption (Bolnick et al., 2003; Dall

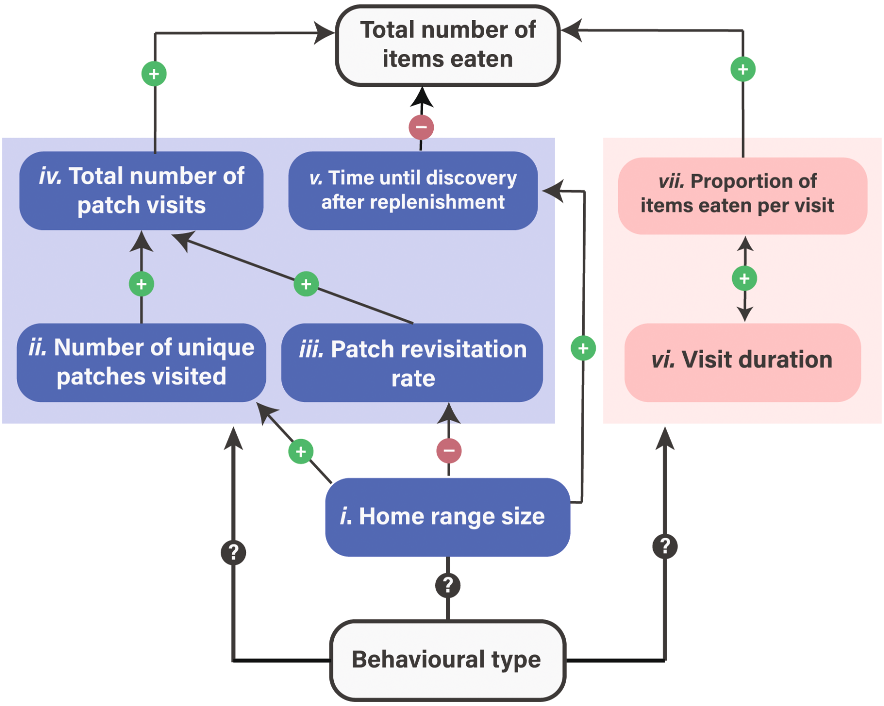

FIGURE 1 Conceptual diagram of components of the foraging process. Behavioural type (BT) effects on foraging success may manifest at different components of the foraging process. BTs may affect home range (HR) size, search patterns within a HR and handling of food once discovered. HR size may have positive effects on the number of unique patches available for an individual, and presumably also revisitation rate. However, individuals with larger HRs may take longer to revisit patches due to further travel distances. Components of the search stage (blue boxes) interact with the handling stage (pink boxes), to determine overall resource consumption. Positive symbols refer to an expected positive relationship between two components, and negative symbols refer to an expected negative relationship. Note that BT effects on foraging are also mediated by further environmental factors (e.g. predation risk, refuge availability and alternative food sources).

et al., 2012). BTs may influence variation in these components (Toscano et al., 2016). HR size, for instance, may be BT-dependent (Payne et al., 2022; Stuber et al., 2022), and many examples document aspects of BT-dependent foraging for active foragers (Mella et al., 2015; Steinhoff et al., 2020). Indeed, recent theory has highlighted how consistent differences in the search for food patches may be particularly important in shaping population dynamics, spatial structure and social networks, largely because they affect encounter rates among individuals and spatial heterogeneity in consumer-resource dynamics (Snijders et al., 2019; Spiegel et al., 2017; Webber et al., 2023).

Here, we investigated BT-dependent foraging in a wild population of sleepy lizards (*Tiliqua rugosa*). Earlier studies of sleepy lizards at our field site demonstrated that individuals exhibit consistent among-individual differences in aggressiveness and boldness over multiple years, and that these behaviours are only very weakly correlated (Payne et al., 2021). Furthermore, we have shown that a lizard's BT can affect its space use, movement and social interaction rates, suggesting that these behaviours should also influence their foraging tactics (Godfrey et al., 2012; Michelangeli et al., 2022; Payne et al., 2022; Spiegel et al., 2015). For example, aggressive lizards tend to use the peripheries of their HR more than unaggressive lizards, which may influence both their encounter rates with conspecifics and food resources (Spiegel et al., 2015). Thus, in this study, we were explicitly interested in decomposing the effects of aggressiveness and boldness (measured in a foraging context) on overall food consumption to their specific effects on the foraging components outlined above (*i–vii*, Figure 1). To test this, we supplemented food in 123 artificial foraging patches across our study site with one of three food abundance treatments (high, low and no-food-controls). Patches were replenished twice a week over the species' entire spring activity season. We quantified lizard search behaviours for these patches using GPS tracking (i.e. *i* – *v*), and we quantified their food handling behaviours using video footage from camera traps at the food patches (i.e. *vi* and *vii*).

Given that more aggressive sleepy lizards have been found to be less responsive to local habitat quality (Spiegel et al., 2015), we hypothesised that more aggressive individuals would respond less strongly to our experimental food array. Specifically, we predicted that they would take longer to locate our artificial foraging patches (i.e. *v*, Figure 1) and consequently consume smaller amounts of the available food (*vii*). Moreover, we expected them to show less differentiation between patches of varying quality (*iii*). In contrast, we predicted that bolder sleepy lizards, who consistently display a stronger tendency to approach food rewards when confronted with potential threats (Payne et al., 2021), would respond more strongly to our experimental food array (thus also providing support for cross-context consistency in boldness). We anticipated that they would be more inclined to exploit all available resources at a foraging patch (i.e. *vii*). Additionally, considering our previous findings of BT-dependent effects on lizard movement and space use (Michelangeli et al., 2022), we also predicted that the most significant impact of BT on foraging performance would occur through its influence on lizard search behaviour (represented by the *ii*–*v* blue boxes in Figure 1).

2 | MATERIALS AND METHODS

2.1 | Study system

Our study site is a ~1.2 km^2 area located near Bundey Bore Station in South Australia (centred on 33°54′16″ S, 139°20′43″ E). The regional climate is dry Mediterranean. Vegetation is chenopod shrubland, dominated by bluebushes (*Maireana sedifolia*), with sparse patches of black oak trees (*Casuarina cristata*). Sleepy lizards (*Tiliqua rugosa*) are large-bodied (27–32 cm adult snout-vent-length [SVL]) (Bull & Pamula, 1996), long-lived skinks that are common throughout the region. They have a diverse diet consisting mainly of annual flowers, berries, and Ward's weed (*Carrichtera annua*), the latter being most common. The sleepy lizard–activity season is largely restricted to the Austral spring (September–December) (Kerr & Bull, 2004) and to periods of the day when ambient temperatures are mild. Adult sleepy lizards at our site are rarely threatened by predators and maintain HRs with core areas shared mostly with the mating partner (Kerr & Bull, 2006; Leu et al., 2011; Payne et al., 2022).

2.2 | Handling and tracking

Starting in late August 2015, we captured 76 adult lizards (mean ± SD initial capture date: Sep 29 ± 14.7 days), representing most of the residents and a subset of the continuous population inhabiting a similar surrounding habitat. Upon initial capture, lizards were sexed, measured for SVL, uniquely identified with toe clips, and equipped with radio-transmitters and GPS tags (Technosmart LTD, Rome, Italy). The tracking apparatus constituted up to 5.2% (typically around 4%) of an average lizard's body weight and has never been observed to have adverse effects on lizard behaviour, movement or body condition (Godfrey et al., 2012, 2013; Leu et al., 2010, 2016; Michelangeli et al., 2022; Payne et al., 2022; Spiegel et al., 2015). Tracking devices were removed at the conclusion of the field season (late December). GPS tags took a location every 2 min during the day (from 06:00 to 19:30). Every 2 weeks, lizards were radio-tracked and recaptured for GPS data downloading and battery replacement, and in three of these occasions they were also brought to a central arena on site for behavioural assays. Tracking continued until tag removal in the first week of December 2015. Overall, we obtained GPS data from 76 lizards, with tracking duration spanning 49.1 ± 15.2 days (mean ± STD, range: 13–77), representing a total of 985,771 GPS fixes.

2.3 | Behavioural assays

To quantify among-individual variation in behaviour, we subjected lizards to two types of standardised assays, following the general approach described in previous studies of our population (Godfrey et al., 2012; Payne et al., 2021; Spiegel et al., 2015) with some minor refinements. The first assay (hereafter 'aggressiveness') involved 'attacking' lizards with a model conspecific. The second assay (hereafter 'boldness') involved offering lizards an unusual food reward (a piece of banana) in the presence of a potential threat (the observer). Individuals differed in their behaviours, ranging from a tendency to flee to a refuge quickly (i.e. being less aggressive and less bold), through intermediate behaviours (showing no obvious response), and up to more aggressive or bolder behaviours that included attacking the model, or approaching the food despite the threat, respectively. During trials, we made several behavioural observations, including movements towards/away from the stimulus, frequency counts of discrete behaviours (e.g. mouth gaping) and timed behaviours (e.g. time to flee). Using these observations as a guide, we gave each lizard a subjective rating (by JK), with higher ratings indicating more aggressive or bolder behaviour. This rating system was previously used to reliably predict a lizard's behavioural type (e.g. Godfrey et al., 2012; Payne et al., 2021; Spiegel et al., 2015) and, importantly, has high among-observer agreement (see Appendix). Lizards were given three trials of each assay with 2 and 3 weeks between repeated trials. Unconditional repeatability for aggressiveness was 0.47 (95% CIs: 0.31–0.59) and 0.21 for boldness (95% CIs: 0.04–0.37). We averaged the three ratings obtained at each trial to create behavioural scores for aggressiveness and boldness for each lizard. We also found no significant correlation between individuals' mean scores in the two traits (Pearson's $r_{(n=72)}=0.16$, $p=0.31$). These estimates are in line with previous work on this study system that have shown that both aggressiveness and boldness are significantly repeatable within and among years ($r\sim0.4$ and $r\sim0.3$, respectively), and only weakly positively correlated suggesting independence between these traits (correlation estimate [95% credibility intervals]: 0.15 [−0.07, 0.39], taken from Payne et al., 2021). Further details on the behavioural assay and including procedures of repeatability estimates of behaviours are given in the Appendix.

2.4 | Food supplementation

Starting on 12 October 2015, we added commercially available cherry tomatoes to 123 food 'patches' at our site. Tomatoes are water-rich yet endure well in dry field conditions, are well within lizards' gape size, are highly conspicuous, and were readily discoverable and edible during pilot observations at an adjacent site. Tomatoes were placed on paper plates inside wire cages attached to the ground to exclude larger herbivores (e.g. sheep), but easily accessible for the lizards. Items were replenished (or replaced if unconsumed) twice a week during the experiment ($N=17$ replacements from October–November 2015) following one of three treatments: high (nine items, $N=50$ patches), low (three items, $N=49$) or control

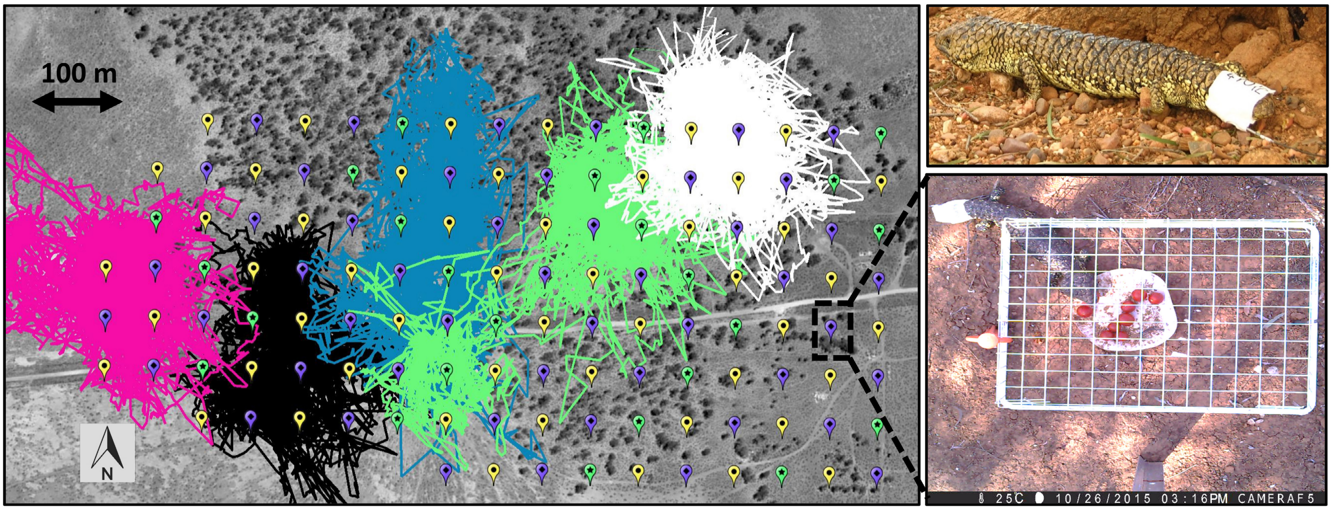

FIGURE 2 Map of the study site with the experimental food patch array. Icon colours refer to different treatments: high (blue), low (yellow) and control (green). The GPS tracks of five lizards have been plotted for reference. The top inset shows a lizard with transmitters attached to the tail; the bottom inset shows a lizard's visit to a food patch as captured by the camera trap.

(no food available, $N=24$). Patches were spaced 50m apart in a grid array (Figure 2), ensuring that each lizard in our study had access to six or more food patches within its HR. Treatments were systematically spread throughout the array in such a way as to avoid neighbouring patches having a similar treatment and so that each lizard would have a mixture of all three treatments in their HR.

2.5 | Camera traps

To quantify lizards' use of the tomato addition array, a subset of patches was monitored with cameras (Browning LTD, model BTC-1XR, $n=27$). Cameras were attached to star pickets and pointed down to provide a birds-eye view of each patch. Cameras were set to time-lapse mode, with a 1-min shooting interval during daylight hours (motion trigger mode was not applicable for these slow-moving lizards). Cameras were alternated among patches every 3weeks. We prioritised patches where we had preliminary indication that visits occurred (e.g. patches with removed tomatoes or nearby lizard activity), while balancing treatments and ensuring representation of control patches. Overall, we monitored a total of 71 unique patches (32 high; 32 low; 7 control). Photographs from the camera traps were observed manually to identify visits to a feeding patch, defined as presence of an animal within one or more (continuous) frames. For each visit we recorded lizard ID (if tagged), entry and departure times (to the nearest minute), and number of tomatoes available before and after the visit.

2.6 | Home range metrics

We used the GPS tracks to determine the lizards' HR, as HR variation may affect the numbers and distribution of available food patches. GPS tracks first were filtered for location errors by excluding fixes with poor accuracy (>3 satellites, horizontal dilution <3 and elevations deviating <50m from the range at our site), and by visual inspection of the tracks for obvious errors. As a proxy for HR size, we used the area of the 95% kernel density estimator (KDE, in hectares) computed as a bivariate normal kernel with an ad-hoc method for the h-smoothing parameter using the 'kernelUD' function in AdeHabitatHR package in R (Calenge, 2011; R Core Team, 2022).

To account for variation in numbers of accessible patches in each lizard's HR, we counted the number of each treatment patch included within a lizard's 95% KDE HR. Note, this count only included patches that were at some point filmed by cameras during the experiment. Whilst the number of each treatment patches in a lizard's HR were considered as separate predictors of a lizard's foraging behaviour, we collectively refer to these hereafter as 'PatchesInHR'. Furthermore, since patch location with respect to a lizard's HR may impact foraging (peripheral patches should be visited less and central patches should be visited more) and patches could occur across multiple HR's, for each patch within each focal lizard's HR we calculated the distance (m) from that focal lizard's HR centre (DistHRc). HR centre was defined as the geometric centroid of the HR polygon.

Finally, to account for the possible effect of social factors on foraging behaviour, for each lizard, we calculated the average extent to which a lizard's HR was overlapped by the HR (utility distribution) of other lizards (hereafter 'PHR'). This measurement excluded lizards with zero overlap with the focal lizard. PHR was calculated using the AdeHabitatHR package in R (Calenge, 2011; R Core Team, 2022). To avoid bias from focal lizards with untagged neighbours, we used the mean PHR rather than the sum.

2.7 | Habitat surveys

To account for effects of local habitat and food conditions on tomato consumption, the habitat around the experimental patches were surveyed from 23 to 29 September using protocols described previously (Spiegel et al., 2015) with some minor modifications. In brief, we surveyed a 40m radius plot centred around each food patch. Using a 1–5 ranking, we characterised for each plot the amount of 'moist food' (i.e. food that was green and edible during survey) and 'refuge quality' (i.e. areas where lizards could shelter). For each ranking, higher scores indicated better conditions. Two observers working together completed the survey, discussing rankings till reaching agreement, and scores were shown to be repeatable and relevant for predicting lizards' space use (see Spiegel et al., 2015 for details). Whilst each ranking was considered as a separate potential predictor of lizard foraging behaviour, we hereafter jointly refer to them as 'Patch resources'. Furthermore, for each lizard, we also calculated a moist food score based on a 40m radius from the central point of a lizard's 95% HR (hereafter 'FoodQualityHR').

2.8 | Ethical note

Lizards were treated using procedures approved by the University of California Davis (protocol 20743) and Flinders University Animal Welfare Committees (protocol E454-17) in compliance with the Australian Code of Practice for the Use of Animals for Scientific Purposes and conducted under permits from the South Australian Department of Environment, Water and Natural Resources to Undertake Scientific Research (A23436). Toe clipping has been used in this lizard study since its inception in 1982 with no detectable adverse consequences. Physiological stress responses (i.e. corticosterone) to toe clipping are several degrees of magnitude lower than stress responses to microchip implants in lizards and are no different from those induced by handling during size measurements (Langkilde & Shine, 2006).

2.9 | Statistics

All models were implemented in a Bayesian framework using the '*brms*' package (Bürkner, 2017), an interface to Stan (Stan Development Team, 2023). We used generalised linear mixed models (GLMMs) when we needed to account for grouping structures in our data (foraging metrics *iii*, *v*, *vi*, *vii*), otherwise we used general linear models (GLMs). To assist with model interpretation, we standardised all continuous predictor variables by subtracting the mean and dividing by the standard deviation. We used regularising priors (as recommended by (McElreath, 2018) and evaluated via prior predictive checks), four chains, and ran models for 2000 iterations with a 1000 warm-up. Note that we were able to use such a low number of samples because Stan models use the No-U-Turn Markov chain Monte Carlo algorithm, which explores parameter space more efficiently and yields much less auto-correlated results than other samplers (Hoffman & Gelman, 2014). All models converged with low among-chain variability (Rhat = 1), and model fit was checked using posterior predictions. Further information on model implementation (e.g. prior specification and sample sizes for each analysis) is provided in the Appendix.

Because we were primarily interested in the effects of each behavioural type (i.e. aggressiveness and boldness) on each stage of the foraging process (total number of tomatoes eaten and, *i–viii* in Figure 1), for each foraging metric, we compared models with the behavioural predictors, including their interaction, versus without these predictors. Thus, for each foraging metric, we considered two competing models (except for patch revisitation rate (*iii*), which had three; see below). We compared competing models using leave-one-out cross-validation (LOO) and model weights. Moment matching was used to improve model assessment when highly influential observations on the posterior were detected by pareto k diagnostics (see Paananen et al., 2021 for details). We report model-averaged predicted means and 95% posterior credible intervals (CIs). Model influence on prediction estimates was weighted by their LOO score. If a single model contained 100% LOO weight, then estimates are only reported from that model. For numeric predictors, we present model-weighted averaged predictions at different values of a relevant predictor.

For all foraging metrics, models included lizard intrinsic traits (i.e. Sex, SVL and in the relevant models also the behaviours), but varied in their other predictors. Below, we briefly outline the model structures for each foraging metric (acronym definitions for predictors can be found in the sections above).

2.9.1 | Total effect of BT on foraging

Total number of tomatoes eaten

We used a zero-inflated Poisson GLM to analyse these count data. The full models included lizard intrinsic traits and PatchesInHR (i.e. number of control, low and high food patches). This was our main response parameter for lizards overall foraging performance, and all subsequent dependent variables were aimed to explain components of the foraging process leading to this one.

2.9.2 | BT effects on search behaviours

(i in Figure 1) Home range size

The full LM assumed a Gaussian error term and only included lizard intrinsic traits as predictors. We did not include PatchesInHR in this analysis because there was no expectation that the addition of the treatment patches will influence a lizard's HR, as we know that their HR's are highly stable among years (Payne et al., 2022).

(ii) Proportion of unique food patches visited

We used binomial logistic regression to estimate the proportion of the total available unique food patches that were visited by each lizard throughout the experiment. Specifically, we modelled the number of successes (i.e. number of unique food patches visited by a lizard), out of 74 trials (i.e. the total number of food patches that were monitored by cameras throughout the experiment and could conceivably be visited by a given lizard). The full model included lizard intrinsic traits, PatchesInHR, FoodQualityHR, PHR and HR size (metric *i*).

(iii) Patch revisitation rate

We used a negative binomial mixed-effects model for these count data (i.e. lizard X returned to patch Y for Z times). The full model included lizard intrinsic traits, food patch treatment (i.e. control/low/high), Patch resources, PHR, DistHRc, HR size and the number of days each food patch were monitored by camera traps. We also considered the two-way interactions between food patch treatment and both behaviours. We included these terms to test whether lizard behavioural traits were associated with a differential response to the different treatments. Thus, we considered three competing models for this foraging metric (a full model, a model without the treatment by behaviour interactions, and a model without the behavioural predictors). Random effects included patch ID and lizard ID.

(iv) Total number of food patch visits

This count variable sums all the visits by a given lizard to all food patches combined. To estimate the effect of the behavioural predictors on this outcome, we used a negative binomial GLM. Lizard intrinsic traits were included in the full model, as well as PatchesInHR, PHR and number of unique patch visits made by a lizard (i.e. metric *ii*).

(v) Time until patch discovery

As tomatoes were replenished in our experimental patches, we calculated the time elapsed between a tomato replenishing event and a lizard's first visit to a given patch after this event. This occurred even if all tomatoes were gone by the time of a given lizard's first visit. This time until discovery (or revisitation when patches are renewed) is an index of lizard search behaviour, with shorter times suggesting a quicker response to food appearance and may imply more efficient search behaviour. Since lizards and cameras were not active during dark hours, these periods were subtracted from calculated time lags in consecutive days. To clarify, only patches that a lizard visited were included, and only for the relevant replenishing event(s). For instance, a data point exists if X hours after replenishing patch Y it was visited by lizard Z. The full GLMM assumed a Gamma process (i.e. time-to-event data) with a log-link function. Model predictors included lizard intrinsic traits, Patch resources, PHR, DistHRc and food patch treatment. We also include an index variable for whether a given visit was a lizard's first to a given patch, as it was expected that a lizard's first discovery of a patch would take longer than all subsequent discoveries (i.e. after the very first patch visit, a lizard was no longer naïve to the presence of the patch). Random effects included patch ID and lizard ID.

2.9.3 | BT effects on handling behaviours

(vi) Patch visit duration

Models assumed a Gamma distribution with a log-link function. The predictors included in the full model included lizard intrinsic traits, Patch resources, FoodQualityHR, PHR, DistHRc and the food patch treatment. We also included an index variable for whether another lizard was observed at the food patch during a focal lizard's visit (hereafter 'Lizard presence'). Random effects included patch ID and lizard ID.

(vii) Proportion of tomatoes eaten per patch visit

This index of the handling stage only included patch visits where tomatoes were available (i.e. did not include control patches or visits to already-depleted patches). We used a binomial GLMM to estimate the proportion of available tomatoes eaten by a lizard per patch visit. Therefore, the number of trials (i.e. number of tomatoes available) could vary between visits. Predictors in the full model included lizard intrinsic traits, Patch resources, FoodQualityHR, DistHRc, PHR, lizard presence and patch visit duration (i.e. metric *vi*). Random effects included patch ID and lizard ID.

3 | RESULTS

The camera dataset included 1968 patch visits by lizards, of which 20% were untagged (almost exclusively at the peripheral patches, suggesting that most adults at our site were tagged). At least 47 different lizards were identified from the photographs. Individual lizards made 27.9 ± 22.3 (3–84; total = 1312) visits at up to 10 different patches, and visits typically lasted less than 5 min (4.2 ± 5.1; 1–39). Almost all monitored patches were visited by lizards. Patches were discovered 652.5 ± 699.1 (2–2861) minutes after food deployment (i.e. the first visit by any lizard to a given patch).

Overall, we found that lizards' BTs affected their foraging. Notably, boldness and aggressiveness had an interactive effect on the total number of tomatoes eaten. Below, we describe how different components of the foraging search and handling stage were affected by these two behavioural traits and their interaction. Tables showing the results from model comparisons and specific model parameter effects for each metric can be found in the Appendix.

3.1 | Total effect of BT on foraging

3.1.1 | Total number of tomatoes eaten

The top model included both behaviours and their interaction (100% LOO weight; Tables S2 and S3). Unless they were also bold, aggressive lizards ate fewer tomatoes than unaggressive lizards (Figure 3). The model predicted that highly aggressive lizards that were shy ate very few tomatoes (only 8.6, 95% CI: 6.5–11.1) but lizards that were aggressive and bold, ate many tomatoes (32.6 tomatoes, 95% CI: 25.7–40.2). In contrast, unaggressive lizards ate a similar number of tomatoes regardless of their boldness score (~25 tomatoes). As expected, lizards with more low and high-treatment patches available within their 95% HR, consumed more tomatoes (Table S3). There was also a comparable positive effect of SVL on tomato consumption (Table S3). Larger lizards consumed more tomatoes than smaller lizards (Figure S2).

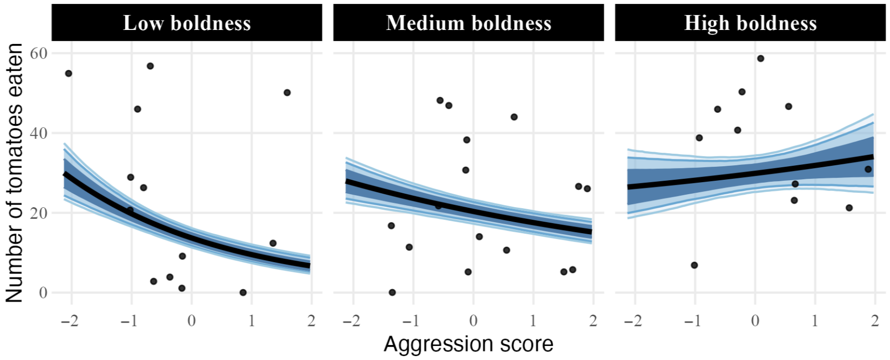

FIGURE 3 Model predicted effect of the interaction between lizard aggression score and boldness score (both standardised) on the total number of tomatoes eaten by a lizard. The figure shows the effect of aggression for low (−1.11), medium (0.07) and high (1.21) values of boldness. Other model predictors were set to their mean or default level (e.g. sex set to female). Circles represent observed data (individual lizards) used in the model for the relevant boldness range (low: $n=13$; medium: $n=16$; high: $n=12$). Blue shading represents 67%, 89% and 95% credibility intervals (from dark to light shading).

3.2 | BT effects on search behaviours

3.2.1 | (*i*) Home range size

The top model included both BTs and their interaction (62% LOO weight; Table S4). Shyer lizards had larger HRs than bolder lizards (Figure 4a). Lizards with the lowest boldness scores had a model-average predicted 95% kernel HR of 4.34 ha (95% CI: 3.27, 5.34) versus 2.87 ha (2.17, 3.52) for lizards with the highest boldness scores (Figure 4a). Aggressiveness and the behavioural interaction had a negligible effect on HR size (Table S5).

3.2.2 | (*ii*) Number of unique food patches visited

The top model did not include the behavioural predictors (92% LOO weight; Table S6); there was no evidence for an effect of either boldness or aggressiveness on the number of unique food patches visited by a lizard (Table S7). Males on average visited more unique food patches than females (male: 4.53 unique patches [3.64–5.44], female: 3.45 unique patches [2.69–4.25]; Figure S3a). Lizards with more low-treatment food patches within their 95% HR visited a higher number of unique food patches (see Figure S3b). In contrast, there was no effect of the availability of the other treatment patches (i.e. control and high) on the number of unique food patches visited (Table S7). Lizards with higher moist food availability in their 95% HR also made slightly fewer unique patch visits (Figure S3c).

3.2.3 | (*iii*) Patch revisitation rate

The top model included the behavioural predictors and their interaction with food patch treatment (81% LOO weight; Table S8). In general, lizards revisited high food patches more regularly than low and control food patches (Table S9; Figure S4b). However, there was a notable negative interaction between aggressiveness and food patch treatment on patch revisitation rate (Figure 5). Unaggressive lizards displayed a strong tendency to preferentially revisit high food patches over low and control food patches (model predicted average revisits; high: 9.10 [3.53–18.9], low: 3.64 [1.44–7.19], control: 2.33 [0.42–6.71]). In contrast, aggressive lizards were less selective in that they revisited high, low and control food patches at similar rates (high: 3.92 [1.51–8.57], low: 4.49 [1.99–8.61], control: 2.83 [0.96–6.37]; Figure 5). As expected, distance from HR centre had a negative effect on lizard patch revisitation rate, implying that peripheral patches in a lizard's HR were less likely to be revisited (Figure S4a), and patch monitoring duration had a positive effect with more revisits detected with longer monitoring (Figure S4c).

3.2.4 | (*iv*) Total number of patch visits

The top model included the behavioural predictors (99% LOO weight, Table S10). Bold lizards visited more food patches than shy lizards (Figure 4b; Table S11). Lizards with the highest boldness scores made a model predicted average of 30.8 [22.5–41.7] patch visits throughout the experiment, whereas shy lizards made an average of 15.5 [9.87–24.4] patch visits. Conversely, aggressive lizards visited fewer food patches than unaggressive lizards (Figure 4c). Lizards with high aggressiveness scores made a model-predicted average of 17.5 [12.2–25.2] patch visits, whereas unaggressive lizards on average made 34.8 patch visits [23.4–51.0]. There was no evidence for an interaction between the two BTs. Surprisingly, the number of available treatment patches within a lizard 95% HR did not influence total patch visits (Table S11).

3.2.5 | (*v*) Time until patch discovery

The top model did not include the behavioural predictors (92% LOO weight; Table S12). There was no evidence for an effect of boldness

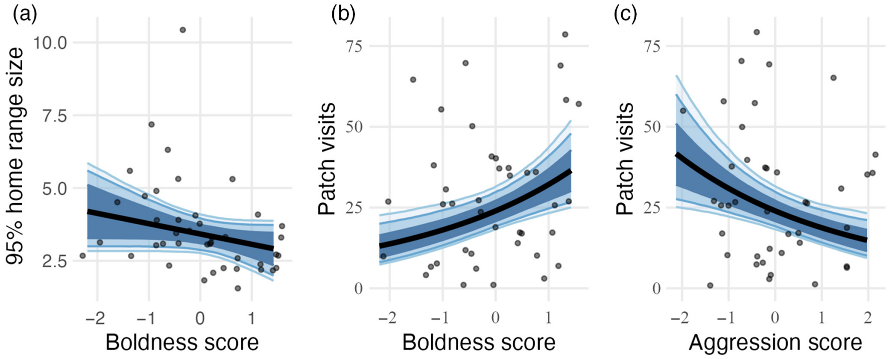

FIGURE 4 Model predicted effect of behavioural type (boldness or aggressiveness, standardised) on (a) 95% home range size, (b and c) total number of visits to foraging patches. Other model predictors (not on the *x*-axis) were set to their mean or default level (e.g. sex set to female). Circles represent observed data (individual lizards) used in models. Shading represents 67%, 89% and 95% credibility intervals (from dark to light shading, respectively).

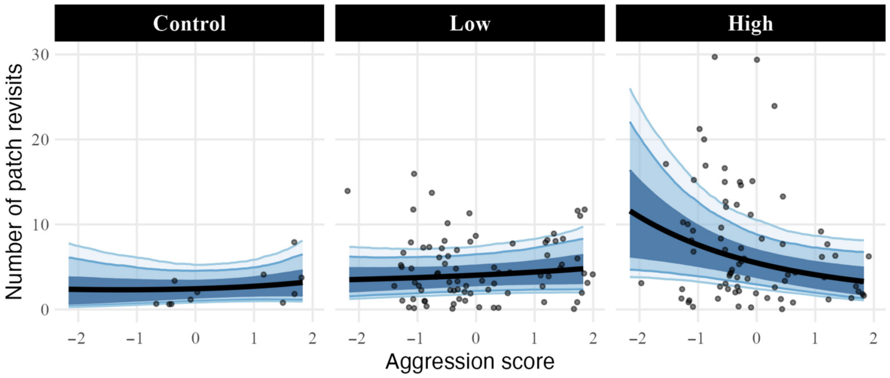

FIGURE 5 Model predicted effect of the interaction between standardised lizard aggression score and food treatment (control, low and high) on the number of revisits to food patches. Other model predictors were set to their mean or default level (e.g. sex set to female). Blue shading represents 67%, 89% and 95% credibility intervals (from dark to light shading). Circles represent the observed number of patch revisits to each treatment (control: *n* = 14; low: *n* = 89; high: *n* = 87). The results show that while non-aggressive lizards revisited high-treatment patches preferably, aggressive lizards did not discriminate between food patches of different quality.

or aggressiveness on time until patch discovery (Table S13). As expected, distance from a lizard's HR centre (DistHRc) had a positive effect on the time it took lizards to find food patches after replenishment, indicating that lizards took a longer time to discover peripheral food patches (Figure S5).

3.3 | BT effects on handling behaviours

3.3.1 | (*vi*) Patch visit duration

The top model did not include the behavioural predictors (92% LOO weight; Table S14). There was no evidence for an effect of boldness or aggressiveness on patch visit duration (Table S15). As expected, lizards visited patches for longer when there were more tomatoes available at the foraging patch (Figure S7). Females on average spent slightly more time at foraging patches than males (Figure S6b). Lizards also spent slightly more time on average at a foraging patch when another lizard was also observed at the patch (Figure S6c).

3.3.2 | (*vii*) Proportion of available tomatoes eaten per patch visit

There was no clear top model, but the model containing the marginally larger weight included the behavioural predictors (52% LOO weight vs. 48% for the alternative model; Table S16). There is some evidence of a positive boldness × aggressiveness interaction (Table S17). Shy lizards ate a lower proportion of available tomatoes than bold lizards if they were also highly aggressive (Figure 6). Lizards that were both shy and aggressive ate on average 33% (19%–49%) of available tomatoes per patch visit, whereas lizards that were shy and unaggressive ate 55% (39%–69%). Bold lizards ate a similar proportion of available tomatoes per patch visit regardless of their level of aggression (Figure 6). Lizards that were both bold and aggressive ate the highest average proportion of available tomatoes per patch visit (72% [55%–84%]). To put these results into perspective, if nine tomatoes were available at a foraging patch, lizards that were both bold and aggressive were predicted to eat 6.3 tomatoes, whereas lizards that are shy and aggressive were predicted to eat 2.9 tomatoes. As expected,

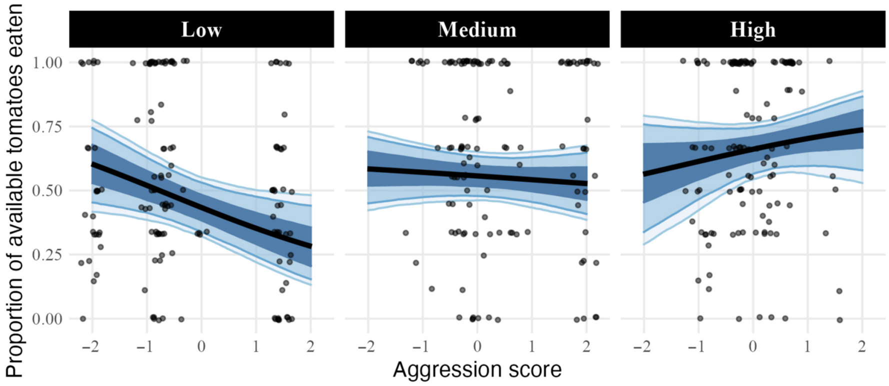

FIGURE 6 Model-averaged predicted effect of the interaction between standardised lizard aggression and boldness scores on the proportion of available tomatoes eaten by a lizard during a patch visit. The figure shows the effect of aggression for low (−1.31), medium (−0.03) and high (1.11) values of standardised boldness. Other model predictors were set to their mean or default level (e.g. sex set to female). Blue shading represents 67%, 89% and 95% credibility intervals (from dark to light shading).

lizards who spent more time at a foraging patch, ate more tomatoes (Figure S8a). Lizards also ate a higher proportion of available tomatoes at the low-treatment patches compared with the high-treatment patches (Figure S8b), simply suggesting that lizards were likely to eat almost all the available tomatoes when fewer were available.

4 | DISCUSSION

Among-individual differences in behavioural traits such as aggressiveness and boldness may affect different search and handling components of the foraging process and underlie population foraging dynamics (Figure 1). Indeed, our detailed analyses of the foraging process under natural field conditions shows the stage-specific and interactive effects of behavioural types (BTs) on foraging success (see Figure 7). We found that bolder lizards ate the most tomatoes from our foraging array because they visited food patches more regularly (*iv* in Figure 7), and ate a higher proportion of the available tomatoes at patches during visits (*vii* in Figure 7). This is true even though bolder lizards also had smaller HRs than shy lizards, and thus access to fewer immediate food patches (*i* in Figure 7). In contrast, aggressive lizards generally ate fewer tomatoes in our foraging array, in part because they discriminated less between high and low-quality food patches when revisiting them (*iii* in Figure 7), and because they visited patches less regularly (*iv*). Unaggressive lizards, in contrast, preferentially revisited high-quality patches, benefiting more from these visits. Importantly, given that the two traits (boldness and aggressiveness) are not correlated to each other and that lizards that were both bold and more aggressive ate the most tomatoes in our experiment, our results suggest that being bold (i.e. more efficient use of available patch resources and more patch visits) may compensate for any lack of foraging opportunities associated with being more aggressive (i.e. poor discrimination between low and high-quality food patches).

4.1 | Boldness and foraging

Our findings are consistent with previous work showing positive correlations between boldness and foraging performance. Bolder (or risk-prone) animals are typically found to forage at higher rates compared with shy individuals because they are more willing to trade off vigilance for food gain, or forage at riskier but less-depleted locations (Eccard et al., 2020; Mazza et al., 2019; Mella et al., 2015; Steinhoff et al., 2020). Sleepy lizards that ate the most tomatoes from our food array were also the individuals that were more willing to approach a food reward in the presence of a potential threat in our standardised boldness assay—providing a robust example of cross-context behavioural consistency. While lizards in our study population do not experience high predation risk, being bold clearly provides an advantage in finding and exploiting food resources. This was true even though bolder lizards have smaller HRs (and thus access to fewer immediate foraging patches; *i* in Figure 7). However, we have previously found that smaller HRs at our study site overlap with areas containing better natural food resources (Michelangeli et al., 2022; Payne et al., 2022), suggesting that the observed positive effects of boldness on foraging also translate into natural situations where food is more patchily distributed. Together, these findings suggest that bolder individuals may deploy an exploitation-type foraging strategy, which may be particularly favourable at our study site where locations of high natural food growth are more predictable but patchily distributed (Spiegel et al., 2017). In other systems where patch locations are less predictable, such a strategy may be less beneficial (e.g. O'Farrell et al., 2019).

4.2 | Aggressiveness and foraging

Unlike boldness, links between aggressiveness and foraging have not been well-studied. Instead, aggressiveness is often linked to variation in sociality as the outcomes of social interactions typically

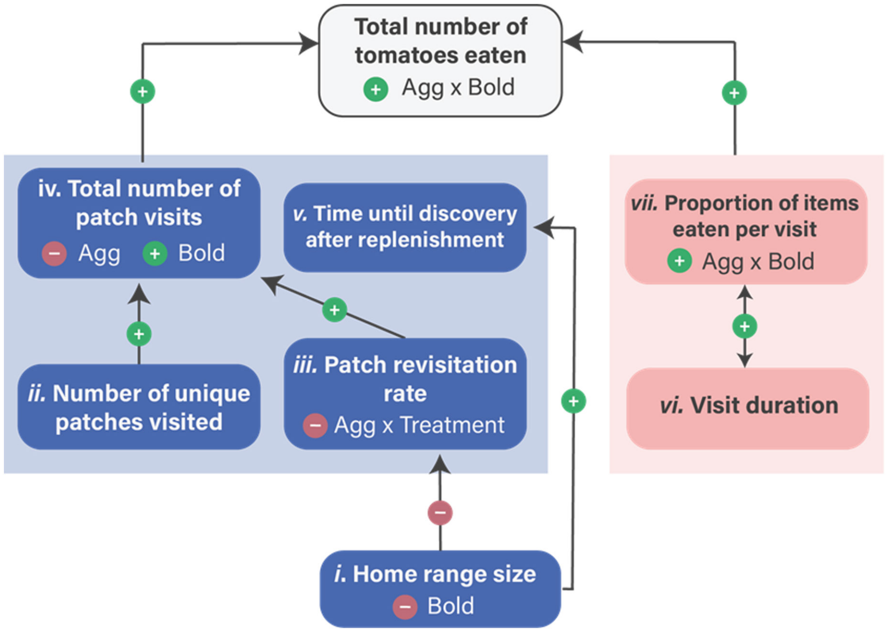

FIGURE 7 Summary of behavioural type (BT) effects on the foraging process. Positive/negative symbols indicate predictor effects on each component. Overall, we found a BT interaction on the total number of food items consumed. Aggressive lizards ate the fewest tomatoes, unless they were also highly bold. Dissecting the contribution of different foraging components shows that BT influenced various aspects of a lizard's search behaviour within their HR (blue boxes) and, to a lesser extent, their handling behaviour at the foraging patch (pink boxes). (*i*) Bold lizards had smaller home ranges (HR) than shy lizards. (*ii*) Larger HRs contained more foraging patches, but this did not affect the number of unique patch visits. (*iii*) Less aggressive lizards had a stronger tendency to preferentially revisit patches with higher food quality over patches with lower food quality, whereas aggressive lizards did not exhibit the same patch-quality discrimination. (*iv*) Bold lizard made more patch visits than shy lizards, whereas unaggressive lizards made more patch visits than aggressive lizards. (*vi*) BT had no clear effect on patch visit duration. (*vii*) Aggressive lizards ate a lower proportion of available tomatoes at a foraging patch unless they were also highly bold. Bold lizards in general ate a higher proportion of available tomatoes at a foraging patch compared with shy lizards.

dictate an individual's level of aggression or avoidance of hostility (i.e. winner-loser effects, Jäger et al., 2019), and these differences may indirectly drive variation in foraging (e.g. Milligan et al., 2017). Indeed, prior work on our study population has shown that aggressive sleepy lizards engage in more agonistic interactions than unaggressive ones (Godfrey et al., 2012), spend more time on the boundaries of their HR where social encounters occur more regularly (Spiegel et al., 2015, 2018) and are less likely to adjust their space use patterns to avoid interactions with conspecifics. Aggressive lizards have also been shown to be less responsive to seasonal changes in natural food availability (Spiegel et al., 2015), which concurs with the current finding that they were poorer at discriminating between high- and low-quality patches in our artificial food array (i.e. *iii* in Figure 7). Together, these results suggest that aggressive lizards may allocate more time patrolling for rival conspecifics at the expense of foraging leading to observed differences in search behaviour (blue boxes in Figure 7) and food handling (i.e. *vii*). More broadly, aggressiveness and territoriality are inherently linked, and opportunity costs associated with territorial defence and aggression have been documented in other species including decreased parental care (Duckworth, 2006) and reduced energy acquisition (Ord, 2021). These findings also concur with theoretical expectations for a trade-off between aggressiveness and investment in foraging and growth (Stamps, 2007).

4.3 | BT-interactive effects on foraging

Our study provides a rare example of interactive effects of behavioural types on foraging performance. This rarity might reflect a methodological bias rather than a biological phenomenon. Most studies exploring the effect of BT on foraging either measure a single BT axis (e.g. either boldness or aggressiveness), are conducted under laboratory conditions (that do not accommodate for environmental variation), or simply do not consider interactive effects of BTs on foraging in their study. Here, we demonstrate that BT effects on foraging performance can occur irrespective of their covariation.

These results concur with our recent study finding a BT-interactive effect on consistent individual movement patterns (Michelangeli et al., 2022). In brief, we found that lizards that were both bold and aggressive exhibited large daily travel distances and high residency times suggestive of HR patrolling behaviour. On the contrary, aggressive, shy individuals exhibited superficial exploratory-like space use (which may explain their poorer performance in the current experiment), and unaggressive lizards spent more time within core areas of their HR where they are less likely to interact with conspecifics. Collectively, these findings suggest that bold, aggressive lizards were likely the most successful foragers in our study because they were good at both excluding competitors from foraging patches (i.e. high aggression), and finding (*iv* in Figure 7) and exploiting (*vii*) available resources (i.e. high boldness). If other lizards (e.g. unaggressive lizards) actively try to avoid hostile interactions, bold, aggressive lizards may have had relatively little competition for foraging patches within their HRs. Conversely, lizards that were both shy and aggressive may have had the lowest foraging success, because they had larger HRs (*i*) requiring more travel between patches and thus lower patch visitation (*iii*), were less selective in their patch choices (*iv*), and did not take full advantage of the available food when visiting a foraging patch (*vii*). In summary, boldness and aggressiveness play different functional roles within our study system, and these differences may underlie variation in movement patterns that could explain our observed BT interactions on overall foraging performance. Future studies can further investigate this topic by assaying exploration (e.g. via an open-field test) and its effect on the overall foraging and particularly on the search phase. Extracting estimates of individual exploration tendency from the movement data itself is also possible (e.g. O'Farrell et al., 2019), but might be limited by the tracking resolution (Nathan et al., 2022).

4.4 | BT-dependent foraging as a link to ecological and social outcomes of behaviour

BT-dependent foraging and movement in our study system likely reflect individual tactics for maximising fitness that have likely been shaped and maintained by social and environmental conditions. Individual difference in movement or search patterns will affect encounter rates with conspecifics and discovery of new resources (Webber et al., 2023). Social experiences play a key role in shaping individual differences in behaviour (Loftus et al., 2021; Montiglio, Ferrari, & Reale, 2013; Montiglio, Garant, et al., 2013; Munson et al., 2021; Sih et al., 2015), and repeated social interactions allow individuals to assess their competitive ability against others (Jäger et al., 2019). Furthermore, knowledge of predictable environmental resources can shape foraging patterns towards an exploitation-type strategy, whereas uncertainty will favour exploration (O'Farrell et al., 2019; Patrick et al., 2017). In our sleepy lizard study population, an individual's level of aggressiveness is likely mediated by their competitive ability and how much they move around and interact with other conspecifics (i.e. engage in agonistic interactions and obtain social feedback). On the contrary, boldness may be linked to an individual's history and knowledge of predictable and reliable resources. Variation in how individuals interact socially or ecologically could give rise to different BT combinations and space use patterns (Webber et al., 2023). For example, high levels of aggressiveness may emerge in bold lizards that have a competitive advantage which they use to 'patrol' and exploit reliable foraging patches, whereas low levels of aggressiveness might develop in bold lizards that do not have a competitive advantage and avoid social interactions by limiting their movements and space use.

The notion that boldness and aggressiveness might affect foraging is not new, both are thought to be among the main axes of behavioural variation that might impact ecological outcomes (Sih et al., 2012; Wolf & Weissing, 2012). Yet, to date we still have limited understanding of the specific alternative pathways that lead to BT-dependent foraging. BTs can affect different aspects of the foraging process, such as the use of social information (Snijders et al., 2019), propensity to attack prey (DiRienzo et al., 2020) and risk-taking behaviours (Mella et al., 2015). Disentangling these effects is essential for understanding their adaptive significance, and how they shape growth and life history traits (Moiron et al., 2020; Montiglio, Ferrari, & Reale, 2013; Montiglio, Garant, et al., 2013), or their consequences for various ecological processes (Sih et al., 2012; Stamps, 2007). Differential foraging among BTs can ultimately link behavioural variation with niche specialisation (sensu Bolnick et al., 2003), in which individuals utilise different resources or habitats that fit better with their foraging tactics, resulting in spatial and/or temporal heterogeneity in resource-consumer dynamics (Allegue et al., 2022; Toscano et al., 2016).

In particular, if BT-dependent searching is a broad phenomenon, it can be associated with recent studies that demonstrate the effects of BT on the exploration–exploitation continuum (Patrick et al., 2017), or differential response to variation in food availability (Herath et al., 2021). In predator–prey interactions, differences in predator search tactics (especially their revisitation rate) can affect the outcome of a predator–prey space use 'games' where whether prey returns to a patch depends on how quickly predators tend to return, and vice versa, how quickly predators return should depend on when prey return (Katz et al., 2013). Furthermore, when space use and activity are BT-dependent, predation rates can depend on the interaction between predator and prey BTs (Toscano & Griffen, 2014). For instance, in jumping spiders unaggressive individuals performed better in encountering predictable prey individuals (Chang et al., 2017). While BT-dependent dispersal and migration are well established (Chapman et al., 2011; Michelangeli et al., 2017), the ecological implications of the association between BT, HR size and search behaviour have gained far less attention (Wat et al., 2020).

5 | CONCLUSIONS

To our knowledge, reports of interactive BT effects on foraging behaviour or foraging success are uncommon, possibly because most individual-level foraging studies to date have been restricted to small spatial scales (e.g. are not conducted in the wild) or to a single behavioural trait. Understanding how intraspecific BT differences translate to ecological functionality (here, through interactive and stage-specific BT effects on foraging) is essential for our ability to predict the consequences of processes that modify population composition by selective removal of certain phenotypes. These include natural processes (e.g. predation, fluctuating environments), and especially human-induced changes, such as invasion (Chapple et al., 2022), and urbanisation (Bar-Ziv et al., 2023). Future directions can explore whether these interactive effects indeed translate to social network position, to parasite transmission and to niche specialisation (e.g. by repeating the experiment with a set of alternative resource types differing in their spatial distribution, rather than merely different quantities of the same one). Future work can also test if these effects drive population density through BT-dependent aggregations (e.g. by habitat matching; Holtmann et al., 2017). Another testable prediction arising from our results is about the differential ability of BTs to cope with local changes in resource distribution and abundance (specifically aggressiveness being less resilient to a change). Given the ongoing changes in land-use and resource distributions, and accumulating evidence on its effect on animal space use (Tucker et al., 2018), identifying these differential responses may prove highly valuable to the conservation of natural systems and maintenance of diversity within and across species.

AUTHOR CONTRIBUTIONS

Orr Spiegel, David L. Sinn and Andrew Sih were responsible for conceiving the idea for the manuscript; Orr Spiegel, Eric Payne, David L. Sinn, Jamie Kirkpatrick, Andrew Sih, Janine-Rose V. Klein and Marco Harbusch collected the data, Marcus Michelangeli and Orr Spiegel conducted the data analysis. Orr Spiegel and Marcus Michelangeli drafted the first version of the manuscript. All authors contributed critically to editing and crafting the final version of the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All datasets and R codes are available through Dryad Digital Repository at https://doi.org/10.5061/dryad.573n5tbgd (Spiegel et al., 2024).

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SUPPORTING INFORMATION

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

Appendix S1: Additional information on behavioural assays and experimental design.

Appendix S2: Additional information on inter-observer agreement and behavioural ratings.

Appendix S3: Additional information on behavioural repeatability calculations.

Appendix S4: Model structures and additional results from statistical modelling.

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