Global Change Biology

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Global Change Biology

RESEARCH ARTICLE OPEN ACCESS

Cross-Continental Analysis Shows That Disturbance Effects on Reptile Body Condition Do Not Predict Abundance Responses

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Received: 28 January 2025 | **Revised:** 16 April 2025 | **Accepted:** 17 April 2025

Funding: This work was supported by the Australian Research Council (LP170101134, AD9031596), the Australian Research Grant Scheme (A18615230), Barrick Kanowna, Charles Darwin University, Edith Cowan University, Holsworth Wildlife Research Endowment, Minerals Research Institute of Western Australia, M.J. Murdock Charitable Trust, Australian Goverment's National Environmental Science Program, Northern Australian Environmental Resources Hub, Norilsk Nickel, Northern Territory Department of Lands, Planning and Environment, OMG Cawse Nickel Operations, Parks Victoria, Placer Dome Asia Pacific Kalgoorlie West Operations, and the Threatened Species Recovery Hub.

Keywords: biodiversity monitoring | fire | habitat fragmentation | invasive species | mining | physiological impacts | population decline | population fitness

Global Change Biology, 2025; 31:e70295
https://doi.org/10.1111/gcb.70295

ABSTRACT

Ecological disturbances are discrete events that alter or transform the physical, chemical, or biological characteristics of ecosystems. Disturbance can cause animal populations to decline and, according to the risk-disturbance hypothesis and population collapse framework, these declines can be predicted by declines in animal body condition. However, no research has empirically examined the general relationship between body condition and abundance, nor their relationship in response to disturbance. We used a combined dataset representing 33 studies and >42,000 observations of 75 species from Australia, New Zealand, Spain and the United States of America to test predictions relating to the relationship between reptile body condition and abundance. We first investigated the relationship at the site level and then used meta-analytical models to test whether populations showed linked changes in abundance and body condition in response to disturbance. We further tested whether key environmental and species traits influenced this relationship and whether there was a time-lagged effect of body condition responses on abundance. We found a positive relationship between mean reptile body condition and abundance at the site level. However, the relationship was largely lost when investigating population responses to disturbance. As such, our results provided no support for the risk-disturbance hypothesis and limited support for the population collapse framework. Therefore, the impacts of disturbance on reptile body condition cannot be assumed to reflect or predict abundance responses. We provide a new conceptual framework that shows how disturbances can modify or uncouple the relationship between abundance and body condition by influencing underlying drivers, such as predation, competition and resource availability. Monitoring programs that infer population impacts based on changes in body condition should first confirm the relationship between these two variables in the relevant study system.

1 | Introduction

Disturbances are discrete events of biotic or abiotic origin that cause either temporary or permanent changes to the physical, chemical or biological characteristics of ecosystems (Battisti et al. 2016). Natural disturbances have played important roles in the functioning and evolution of ecosystems for millions of years (Battisti et al. 2016; Pausas and Keeley 2009). More recently, though, anthropogenic disturbances have proliferated globally, including human disruption of natural disturbance regimes (IPBES 2019; Parmesan et al. 2022). Disturbances can have direct effects on wildlife, such as injury, infection or mortality, as well as indirect effects via altered environmental conditions, habitat structure, food resources and species interactions (Santos et al. 2022; Sergio et al. 2018).

Research into the effects of disturbance on wildlife has focused primarily on community and population level responses (Cordier et al. 2021; Hillebrand and Kunze 2020; Keinath et al. 2017; Quesnelle et al. 2014; Sousa 1984). Response metrics such as species richness and occupancy provide insight into the loss and gain of species following disturbance, while measures of abundance provide insight into changing population size (Deng et al. 2023; Williams et al. 2022). On the other hand, individual response metrics of animal health or fitness can encompass indirect effects of disturbance by considering the effects on individuals persisting in disturbed landscapes. As such, individual response metrics are expected to act as an early indicator of future population change (Cerini et al. 2023). For instance, lower body condition of male white-plumed honeyeaters (*Ptilotula penicillatus*) following heat exposure reduced their probability of survival in the following spring (Gardner et al. 2016).

Body condition is an individual response metric that acts as a proxy for energy stores and fitness (ability to survive and reproduce) (Labocha et al. 2014). This metric is typically calculated using the mass and size of individual animals, making it an easily accessible indicator of health compared to other alternatives (e.g., stress or immune function measures). Given the connection between body condition and reproductive success (Lannoo and Stiles 2017; Reading 2004; Testa and Adams 1998), and body condition and mortality risk (Aubry et al. 2013; Shine et al. 2001; Stewart et al. 2021), the effects of disturbances on body condition are often thought to reflect broader population responses (e.g., Cerini et al. 2023; Cogălniceanu et al. 2021; Janin et al. 2011; Macdonald et al. 2023). However, the generalized relationship between body condition and abundance is poorly resolved (Gould et al. 2024; Macdonald et al. 2023).

The risk-disturbance hypothesis and population collapse framework predict that population declines follow reductions in individual body condition (Cerini et al. 2023; Frid and Dill 2002). The risk-disturbance hypothesis predicts that the impacts of disturbance on individuals will be characterized by changes in perceived risks, analogous to predation risk, where animals become hypervigilant, but at the cost of foraging and reproductive success (Frid and Dill 2002). Similarly, the population collapse framework uses individual body condition, along with other individual response metrics, to predict both concurrent and future population collapse following environmental stress (Cerini et al. 2023). Both frameworks acknowledge important assumptions and caveats, but to date, little work has explicitly tested these predictions.

A positive relationship between body condition and population abundance is expected because individuals with poor body condition can have lower fitness and higher mortality, leading to population declines (e.g., Lannoo and Stiles 2017; Madsen et al. 2023; Reading 2004; Shine et al. 2001). On the other hand, a negative relationship between body condition and abundance could arise when the relationship is driven by intra-specific competition (Herrando-Pérez et al. 2012; Stewart et al. 2005). However, there are few long-term studies explicitly assessing the links between body condition, demography, and population growth trajectories (e.g., Gardner et al. 2016; Pigeon et al. 2017; Reading 2007). Of the few studies investigating the concurrent impacts of disturbances on body condition and population metrics, some have found a positive relationship (Emery et al. 2021; Keehn et al. 2019; Lunghi et al. 2018;

Smith 2018), no relationship, or a negative relationship (Gould et al. 2024; Grimm-Seyfarth et al. 2018; Keyser et al. 2005; Laidre et al. 2006; Welsh et al. 2008). Furthermore, there can be time lags, with body condition an important predictor of annual survival in the following activity period (Madsen et al. 2023). This range of responses reported in the literature emphasizes the need for further research and empirical synthesis.

Reptiles provide a particularly good model for addressing this research question; they are widespread globally, ecologically important, relatively easy to capture compared to other vertebrates (e.g., birds), and the data needed to calculate body condition are relatively simple to collect (Cox et al. 2022; Macdonald et al. 2023; Schwarzkopf 2022). Many reptiles are threatened by habitat disturbances such as fire, invasive species, drought, and habitat fragmentation (Böhm et al. 2016; Cox et al. 2022; Tingley et al. 2019). Conversely, some reptile species rely on regular disturbance to maintain suitable habitat. For example, Indigenous fire management in Australia and fire restoration in the United States of America can promote reptile diversity by creating habitat for early successional species (Fair and Henke 1997; Legge et al. 2024). Global meta-analyses have shown that disturbances generally have negative impacts on reptile body condition (Macdonald et al. 2023) and abundance (Doherty et al. 2020). However, there was a high level of unexplained variance in the results of these studies (Doherty et al. 2020; Macdonald et al. 2023) and no research has systematically investigated the relationship between body condition and abundance responses to disturbance for any taxonomic group.

Life history traits and environmental characteristics can be important mediators of wildlife responses to disturbance (Sergio et al. 2018), including effects on abundance and body condition. Disturbance characteristics, such as disturbance type and time since disturbance, could influence how carrying capacity is affected and, in turn, determine whether abundance and body condition show similar or different responses to disturbance. For example, disturbance types that result in direct mortality (e.g., invasive predators) may not influence carrying capacity, whereas disturbances that reduce habitat (e.g., logging) can reduce carrying capacity. In addition, populations exposed to press disturbances (i.e., ongoing, continuous disturbances, such as invasive species or climatic change) may be able to adapt behaviorally to regain and maintain body condition (Rodríguez-Prieto et al. 2010). Species traits could also influence behavioral responses to disturbance, which in turn could affect body condition and abundance (Böhm et al. 2016; Lazzari et al. 2022).

Examining the relationship between reptile abundance and body condition and their relationship with disturbance provides an opportunity to test the risk-disturbance hypothesis and population collapse framework (Cerini et al. 2023; Frid and Dill 2002). We combined more than 42,000 data points from 33 studies across 75 reptile species to test the following three predictions:

1. Average individual body condition will be positively associated with abundance at the site-survey level, reflecting the mechanistic relationship between body condition, survival, and reproduction (Cerini et al. 2023; Reading 2004; Shine et al. 2001).
2. Body condition responses to disturbance will be positively correlated with abundance responses to disturbance, indicating that individual fitness consequences drive population change (Cerini et al. 2023; Frid and Dill 2002). Alongside this prediction, we investigated the potential role of disturbance characteristics and species traits in influencing the relationship between the two metrics.
3. As an alternative to prediction 2, body condition responses to disturbance in one year will be positively correlated with abundance responses to disturbance in the following year due to time-lagged effects of body condition on population growth, such as changes in reproductive output (Gardner et al. 2016; Madsen et al. 2023).

2 | Methods

Between October and December 2023, suitable datasets were identified through three main methods: (1) reviewing the data sources of a recent global meta-analysis investigating reptile body condition responses to disturbance (Macdonald et al. 2023), (2) using 'Scopus' to identify prominent authors publishing in the field of reptile abundance responses to disturbance, and (3) asking existing networks and research collaborators for recommendations. Adopting a formal systematic review approach was not suitable for this study because it was necessary to use individual animal and site-survey level data (often unpublished) and to consult with the data custodians (author group) regarding data cleaning and interpretation.

Datasets were deemed suitable for our research questions and meta-analytical approach if they (1) systematically surveyed reptiles (e.g., live trapping, timed searches) in both disturbed and undisturbed sites and (2) recorded count data at the species level and individual snout-vent length and weight measurements.

We formed a research collaboration that brought together 33 existing datasets meeting our research requirements (see Table S1 AND S2, "Data Sources," and Macdonald 2025 for secondary dataset details). These datasets came from studies in Australia, New Zealand, Spain, and the United States of America, which investigated 10 disturbance types across 75 reptile species from 13 families (Table S3).

2.1 | Data Processing

We used the R software for all data processing and analysis (R Core Team 2022). For the abundance data, recaptured individuals were excluded from datasets when recorded. In addition, in datasets where sampling effort varied across sites, counts were converted to capture rates by standardizing counts by a unit of survey effort. As such, capture rates were used as a proxy of relative abundance.

For body condition data, we excluded gravid and deceased individuals (when recorded) to avoid potential weight confounding. In addition, we removed suspected measurement or data entry errors. To identify likely errors, we (1) visually assessed the range of raw snout-vent and mass values against known species information to identify clear outliers, (2) visually assessed scatterplots of mass and snout-vent length, and (3) visually assessed the distribution of Scaled Mass Index values (explained below). Individuals with greater than double or less than half the mass of individuals of a similar snout-vent length size were excluded. The final Scaled Mass Index was calculated after errors were excluded from datasets.

2.1.1 | Scaled Mass Index

The Scaled Mass Index (SMI) is a calculation of body condition that controls for the allometric relationship between mass and growth and is robust to sexual size dimorphism (Peig and Green 2010). SMI scales the mass of individuals to the mean length of the population along a population specific allometric relationship between length and mass. Therefore, SMI values are in mass units, making results easily interpretable. We used the methods from Peig and Green (2009) to calculate the SMI of each species within each dataset. We fitted standardized major axis models using the log(mass) and log(snout-vent length) of populations using the SMTR package v3.4–8 (Warton et al. 2012). We then used the slope coefficient from the model outputs as the scaling coefficient (b_{SMA}) in subsequent SMI calculations:

$$\widehat{M}_i = M_i \left[\frac{L_0}{L_i}\right]^{b_{\text{SMA}}}$$

where the scaled mass of an individual ($\widehat{M}_i$) is calculated using the mass of an individual (M_i), the mean snout to vent length (L_0), the snout to vent length of the individual (L_i) and the slope coefficient from the standardized major axis model (b_{SMA}).

2.2 | Site-Survey Dataset

To investigate the relationship between relative abundance and body condition, we compiled a dataset of site-survey responses (Figure 1). For each species within each study, we compiled capture rates and the mean SMI for each site-survey when there were at least three individuals with SMI values. We excluded populations that had fewer than three site-surveys with mean SMI values. After processing, this dataset contained 1837 site-survey records.

2.2.1 | Site-Survey Analysis

To investigate the relationship between body condition and relative abundance, we fitted linear mixed models using the site-survey dataset (Figure 1). We used the log(mean SMI) of each site-survey as the response variable and inversely weighted the model with the SMI standard error. We used site-survey reptile capture rates as the predictor variable in models. Capture rates were scaled at the species level per dataset to standardize capture rates across studies (mean of zero and standard deviation of one). We included "dataset ID," "site" nested within "dataset ID," "species" nested within "dataset ID" and a phylogenetic distance matrix as random effects in the model to account for potential non-independence within and across the underlying datasets. We created the phylogenetic matrix using all study species from phylogeny trees obtained from the Vertlife database (Tonini et al. 2016). We first fitted a model with the site level capture rate as the sole predictor variable.

We fitted a second model investigating the interaction between capture rates and "disturbance" (levels: yes, no) to compare the relationship between relative abundance and body condition in disturbed sites and reference sites. We used the same random effects structure as in the previous model and a subset of the data that included populations with three or more site-surveys within a "disturbance" level. We fitted site-survey models using the Almer package (Bolstad et al. 2014). These models are unable to account for imperfect detection within the underlying datasets. Data and R code are available in Dryad (Macdonald 2025).

2.3 | Population Response Dataset

To investigate the relationship between body condition and relative abundance responses to disturbance, we compiled a population response dataset (Figure 1). For each species within each

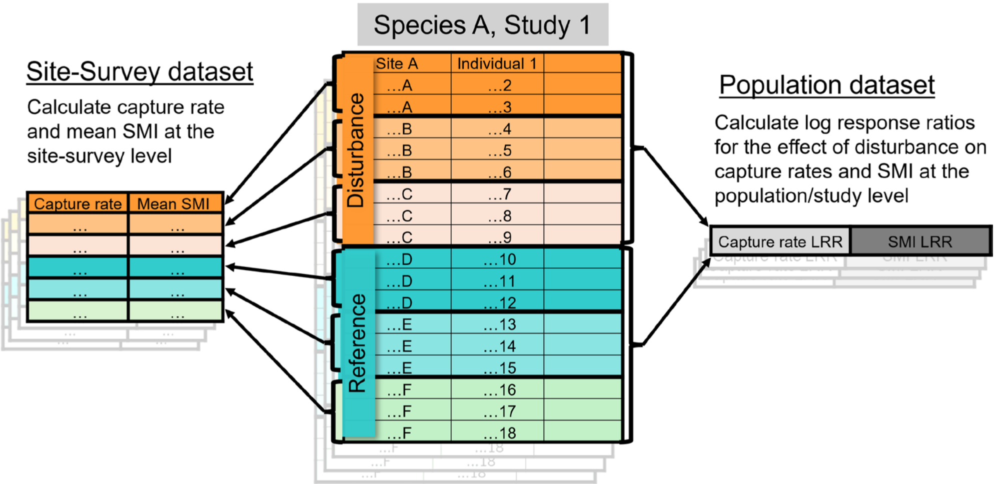

FIGURE 1 | Overview of how the site-survey and population response datasets were created from original studies. LRR: Log-Response Ratios, SMI: Scaled Mass Index.

study, we calculated log-response ratios (LRR) for both SMI and capture rates to standardize our response and predictor variables across the underlying datasets. We calculated LRRs and their associated variances using the SingleCaseES package v0.7.2 (Pustejovsky et al. 2023). LRRs reflect the proportional change in response metrics between disturbance and reference values. For example, a negative abundance LRR reflects lower mean relative abundance within disturbed sites compared to reference sites, while a positive abundance LRR reflects greater mean relative abundance within disturbed sites compared to reference sites.

We excluded populations that had less than five reference or disturbed individuals. When datasets contained distinct repeat sampling (e.g., yearly surveys), LRRs were calculated across sites and individuals for each survey period independently. However, in one study (SW_01) there was one reference and one disturbance site, surveyed for three years. As such, we treated data from years as replicates, like sites in other datasets, and calculated LRRs by comparing the three unburnt surveys with the three burnt surveys.

When individual datasets included secondary variables which could introduce potential variation in the responses (e.g., vegetation type), we controlled for those secondary variables using the *aggregate* function within the LRR calculation (Pustejovsky et al. 2023). Likewise, when datasets contained a crossed design with multiple disturbance types, we calculated LRRs for each disturbance type with the other disturbance types controlled for within the aggregate function. After processing, this dataset contained 282 pairs of LRRs, created from 42,703 records.

2.3.1 | Population Response Analyses

We fitted meta-regression models to investigate the relationship between abundance responses to disturbance, and body condition responses to disturbance. We used a robust variance estimator, contained the degrees of freedom to the number of datasets (33) and used restricted maximum likelihood. To account for potential non-independence across effect sizes, we included the random effects; "dataset ID," "species," "species" nested within "dataset ID" and a phylogenetic distance matrix (Tonini et al. 2016) in each model. The capture rate LRR and associated variances were used as the response variable in our models. We included the linear and quadratic terms of body condition LRR as the predictor variables to investigate the relationship between these response metrics.

We subsequently fitted models that investigated how capture rate LRRs (response variable) were affected by the interaction between the linear or quadratic body condition LRR term and additional predictor variables. Additional predictor variables were disturbance group (levels: pulse, press), time since disturbance (pulse disturbance only), reproduction mode (levels: live bearing, egg laying), species body size (snout-vent length) and disturbance type (Table 1). For disturbance type, we limited the dataset to disturbances that contained more than 15 effect sizes from more than three datasets (combined), namely fire, habitat fragmentation, invasive species, and mining restoration. Most of our studies investigated the impacts of fire (44% LRRs, 43% studies). Therefore, we ran an additional model investigating the interaction between body condition LRR and time since disturbance for fire data only.

To evaluate whether abundance responses to disturbance were related to body condition responses to disturbance from the previous year, we subsetted the population response dataset to include only studies with repeat annual surveys. We then paired population abundance LRR with the body condition LRR from the previous year. This dataset contained 69 pairs of LRRs, created from 10,250 records across 10 studies. Using the same model structure, we fitted meta-regression models using the body condition LRR from the previous year as the predictor variable. We used the metafor package v3.8–1 (Viechtbauer 2010) to fit all meta-regression models. These models are unable to account for imperfect detection within the underlying datasets. Data and R code are available in Dryad (Macdonald 2025).

2.3.2 | Sensitivity Analysis

To assess the robustness of our population response analysis, we ran two types of sensitivity analyses on the meta-regression models: Cook's distance outliers and body condition variance. When results were significant ($p < 0.05$) we assessed the influence of outliers using Cook's distance values by refitting the models without each effect size that had a Cook's distance value > 1 and again without all effect sizes with a Cook's distance > 1 (Viechtbauer and Cheung 2010).

In the population response dataset, each SMI LRR value had an associated variance that could not be accounted for in the meta-regression models. For body condition variance sensitivity, we refitted the models after excluding data with large SMI LRR variance (mean + 2 SD), that is, lower confidence.

3 | Results

3.1 | Site-Survey Responses

We found a significant positive relationship between the mean Scaled Mass Index (SMI) and scaled capture rates at the site-survey level ($\beta \pm \mathrm{SE} = 0.009 \pm 0.003$, $t = 3.22$, $p = 0.002$), whereby an increase in capture rates of one standard deviation corresponds with a SMI increase of one gram. We found that mean SMI was significantly lower in disturbed sites compared to undisturbed sites ($F_{1,39} = 8.45$, $p = 0.006$). However, we found no evidence for an interactive effect between scaled capture rates and disturbance (levels: yes, no) ($F_{1,39} = 0.406$, $p = 0.528$).

3.2 | Population Responses

At the population level, we found a relatively even spread of congruent responses (where disturbance had either a positive or negative effect on both mean abundance and mean body condition) and contrasting responses (where disturbance had an opposing effect on the two metrics) (Figure 2a).

TABLE 1 | Disturbance characteristics and species traits, with justifications on how they may impact abundance and body condition responses to disturbance.

Variable	Justification
Disturbance group levels: press, pulse. Press: Fragmentation, Grazing, Invasive Species, Land cover change, Urbanisation, Wind turbines. Pulse: Drought/Low rainfall, Fire, Logging, Logging/Fire, Mining rehabilitation	Lizards can adapt to disturbed landscapes and regain lost body condition (Rodríguez-Prieto et al. 2010). Therefore, we might expect weaker body condition responses following disturbances which are ongoing (i.e., press disturbances) compared to pulse disturbances which are acute, and which habitats can recover from
Time since disturbance (years). Pulse disturbances only	Resource availability can change with time since disturbance, often defined by post disturbance successional trajectories (Hutchinson 1941)
Disturbance type levels: Drought/Low rainfall, Edge, Fire, Fragmentation, Grazing, Invasive Species, Land cover change, Logging, Logging/Fire, Mining rehabilitation, Urbanisation, Wind turbines	Reptile abundance and body condition responses can differ across disturbance types (Doherty et al. 2020; Macdonald et al. 2023). The influence of disturbance may differ between metrics. For example, disturbance types that destroy food resources may have greater influence on body condition than abundance
Reproduction mode (levels: live bearing, egg laying)	Macdonald et al. (2024; unpublished data) found similarities in the body condition and abundance responses of two live bearing species. Live bearing species have greater basking and foraging requirements, lower reproduction rates, and slower population recovery compared to egg laying species (Lazzari et al. 2022; Meiri et al. 2012; Robert and Thompson 2007). Therefore, disturbances may have larger effects on the body condition of live bearing species compared to egg laying species
Body size (mean species snout-vent length)	Although it was not an important predictor of reptile body condition or abundance responses to disturbance at the population level (Doherty et al. 2020; Macdonald et al. 2023), it is not known whether body size has a deterministic effect on the relationship between abundance and body condition in response to disturbance. Smaller species may be more likely to survive disturbance events (Böhm et al. 2016), but the reduction in resources and limited ability to emigrate may increase intra-specific competition for small species, while any surviving individuals of large species may have increased mobility and access to potential resources

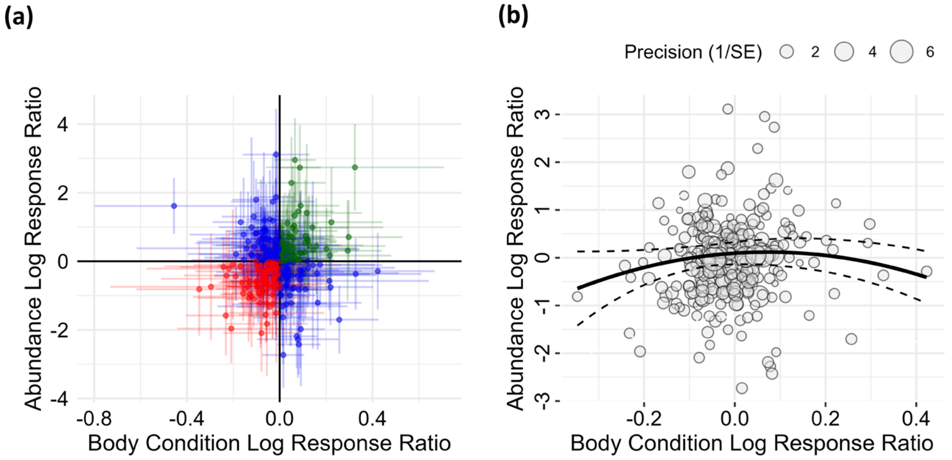

FIGURE 2 | (a) Log-response ratios of abundance and body condition responses to disturbance and 85% confidence intervals. Disturbance had a negative (red), positive (green) or variable (blue) effects on abundance and body condition. (b) Body condition variance sensitivity analysis investigating the quadratic body condition log-response ratios (LRR) against abundance LRR. Dataset excludes effect sizes with large body condition LRR variance (mean + 2 SD). Dashed lines: 95% confidence intervals.

We found no overall relationship between abundance log-response ratios (LRR) and linear ($\beta \pm \text{SE} = 0.323 \pm 0.47$, $p = 0.495$) or quadratic ($\beta \pm \text{SE} = 1.620 \pm 3.48$, $p = 0.645$) body condition LRR. However, when assessing body condition variance sensitivity by excluding results with high SD (see Section 2.3.2 Sensitivity Analysis), we found a significant non-linear relationship between SMI LRRs and abundance LRRs, whereby larger body condition responses to disturbance (both positive and negative) were associated with negative abundance responses to disturbance ($\beta \pm \text{SE} = -4.324 \pm 1.90$, $p = 0.030$, Figure 2b).

3.2.1 | Disturbance Group

We found no evidence for a linear relationship between abundance and body condition LRRs when disturbance group (press/pulse) was included in the model ($\beta \pm \text{SE} = -0.002 \pm 1.19$, $p = 0.999$), nor when assessing body condition variance sensitivity (see Section 2.3.2 Sensitivity Analysis).

Abundance LRR was significantly affected by a non-linear interactive effect between body condition LRR and disturbance group, whereby larger body condition responses to disturbances were associated with positive abundance responses to press disturbances, but with negative abundance responses to pulse disturbances ($\beta \pm \text{SE} = -15.91 \pm 2.62$, $p < 0.001$, Figure S1). When excluding Cook's distance outliers (see Section 2.3.2 Sensitivity Analysis), the inference of the results remained the same. However, the relationship was lost when assessing body condition variance sensitivity (see Section 2.3.2 Sensitivity Analysis).

3.2.2 | Disturbance Type

We found no linear relationship between abundance and body condition LRRs when we included disturbance type in the model ($F_{7,19} = 1.22$, $p = 0.339$), including when we assessed sensitivity to body condition variance (see Section 2.3.2 Sensitivity Analysis).

We found a significant non-linear interactive effect between body condition LRR and disturbance type, whereby larger positive and negative body condition LRRs for fragmentation and invasive species were associated with positive abundance LRRs ($F_{6,15} = 15.28$, $p < 0.001$, Figure S2). The inference of the results remained largely the same when individual Cook's distance outliers were removed (see Section 2.3.2 Sensitivity Analysis). However, the relationship disappeared when all Cook's distance outliers were removed and when assessing body condition variance sensitivity (see Section 2.3.2 Sensitivity Analysis).

3.2.3 | Time Since Disturbance

We found no linear or quadratic relationship of abundance LRR with the interaction between body condition LRR and time since disturbance, nor in any sensitivity analyses (linear: $\beta \pm \text{SE} = 0.06 \pm 0.21$, $p = 0.778$, quadratic: $\beta \pm \text{SE} = 1.17 \pm 1.37$, $p = 0.421$). Likewise, we found no relationships between abundance and body condition LRRs with time since disturbance for fire datasets only (linear: $\beta \pm \text{SE} = 0.02 \pm 0.21$, $p = 0.923$, quadratic: $\beta \pm \text{SE} = 1.07 \pm 1.22$, $p = 0.411$).

3.2.4 | Species Traits

We found no relationships between abundance and body condition LRRs when investigating the interactive effects with body size (linear: $\beta \pm \text{SE} = 0.003 \pm 0.003$, $p = 0.402$, quadratic: $\beta \pm \text{SE} = -0.02 \pm 0.02$, $p = 0.306$), or reproductive mode (linear: $\beta \pm \text{SE} = 0.63 \pm 1.27$, $p = 0.623$, quadratic: $\beta \pm \text{SE} = -0.25 \pm 3.18$. $p = 0.937$), nor in any sensitivity analyses.

3.2.5 | Previous Years' Body Condition

We found no evidence for a relationship between abundance LRR and body condition LRR from the previous year (linear: $\beta \pm \text{SE} = 0.62 \pm 0.727$, $p = 0.421$, quadratic: $\beta \pm \text{SE} = -8.94 \pm 7.69$, $p = 0.283$), nor in any sensitivity analyses.

4 | Discussion

Our results reveal a positive relationship between reptile capture rates and body condition at the site-survey level. The implication of these results is that population size is more likely to be driven by individual fitness compared to density dependence (Herrando-Pérez et al. 2012). These results align with some past research that found lower reptile body condition was associated with lower reproductive output and higher mortality risk (Reading 2004; Shine et al. 2001). However, the results were also highly variable, which aligns with research by Lee-Yaw et al. (2022) who found that species distribution models had poor predictive capacity for a range of community, population, and individual response metrics. Overall, our site-survey results provide only limited support for our first prediction. They also provide limited support for the population collapse framework by showing a concurrent relationship between the two metrics (Cerini et al. 2023).

Environmental variables may weaken the relationship between body condition and abundance by having strong but variable influences on each response metric. For example, in Australia, *Gehyra variegata* (gecko) population size and body condition were strongly influenced by different climatic factors; summer temperature and rainfall were important drivers of population size, whereas winter rainfall and river height were important drivers of body condition variation (Grimm-Seyfarth et al. 2018). Such results highlight the potential for idiosyncratic responses across studies to weaken the expected positive relationship between body condition and abundance.

4.1 | Population Responses to Disturbance

We found little evidence for a relationship between reptile abundance and body condition responses to disturbance (Figure 2). Our population results provided no support for our second or third predictions and, as such, no systematic overall support for the risk-disturbance hypothesis (Frid and Dill 2002) or the population collapse framework (Cerini et al. 2023). Disturbances may modify or uncouple the relationship between abundance and body condition by influencing underlying drivers, including predation, competition, and resource availability (Figure 3). These drivers can, in turn, influence species behavior (e.g., foraging and dispersal) and mortality risk (Figure 3). For example, fire can alter predator–prey dynamics (Doherty et al. 2022) which may, in turn, influence population size via direct predation and influence

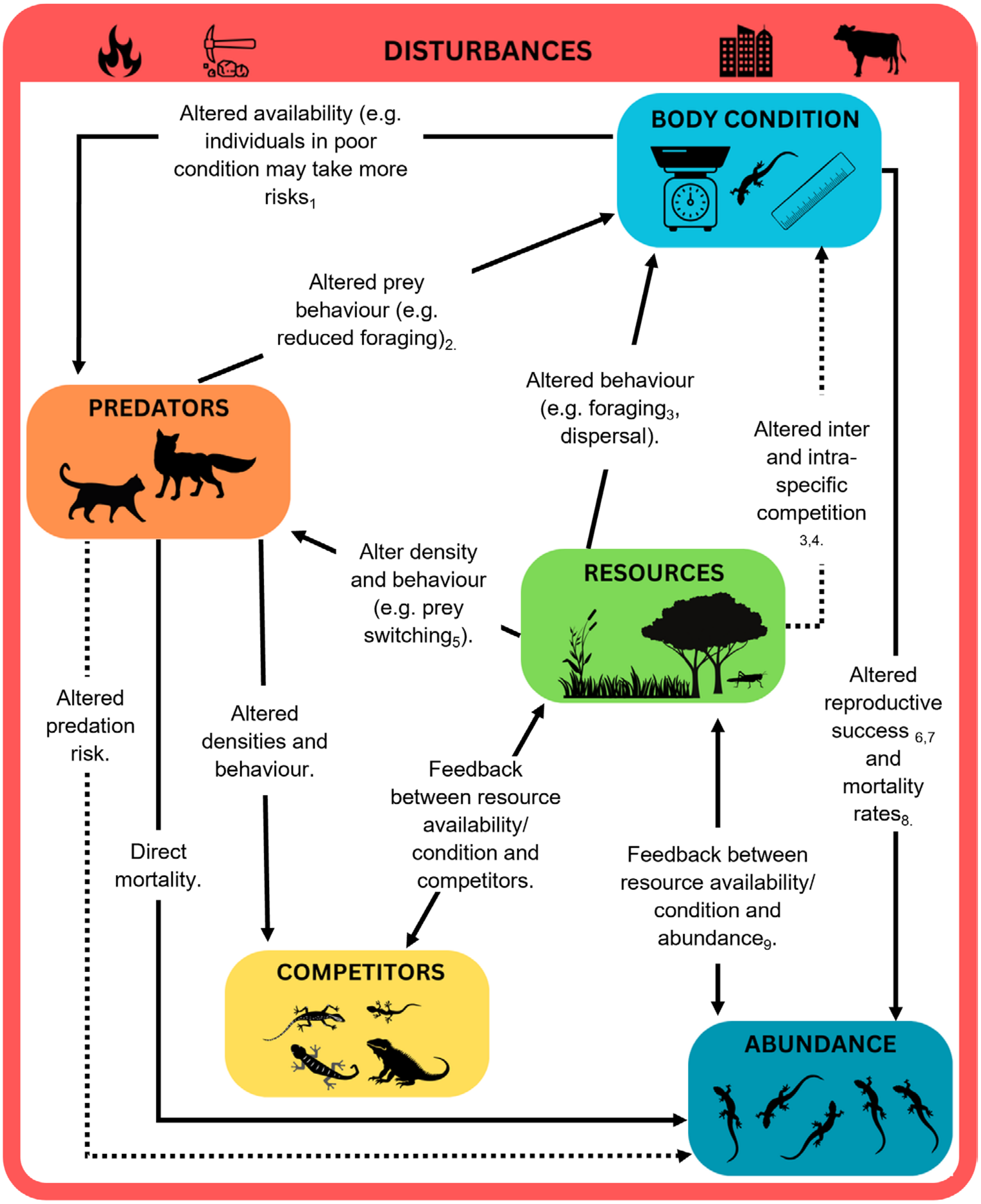

FIGURE 3 | Hypothesized causal links between reptile body condition and abundance and the additional influence of resources, competitors, and predators on this relationship. Disturbances and other abiotic factors can also influence these pathways and interactions. Solid arrows indicate direct links, while dashed arrows indicate indirect links. [1]Heithaus et al. (2007), [2]Amo et al. (2006), [3]Stewart et al. (2005), [4]Keyser et al. (2005), [5]Catling (1988), [6]Lannoo and Stiles (2017), [7]Reading (2004), [8]Shine et al. (2001), [9]Walkup et al. (2017).

body condition via changes in foraging behavior or competition (Figure 3). Likewise, recent work found that invasive predator management could have a strong influence on reptile abundance (unpublished data from Macdonald et al.), while having little effect on reptile body condition (Macdonald et al. 2024). These contrasting results could be explained by greater predator densities influencing the behavior and densities of target species and their competitors, while changes in direct predation concurrently reduced intra-specific competition (Figure 3). Future research should examine the key drivers influencing the relationships between response metrics, particularly predators, competitors, and changes in resource availability (Figure 3). Understanding how key drivers influence population carrying capacity and via which mechanisms (e.g., changes in population size, foraging, thermoregulation or dispersal) may improve predictive frameworks that are important in conservation management (Cross et al. 2021; Gibbons et al. 2000; Pulsford et al. 2016). This work would be especially valuable for species where disturbance is known to lead to population collapse (Walkup et al. 2017). These mechanisms could be explored using natural field experiments as well as experimental approaches (e.g., in mesocosms or enclosures) that control resource availability or population densities under disturbed conditions (Baruah et al. 2019).

Disturbances can alter the relationship between response metrics. For example, Sinclair et al. (2023) found that anthropogenic effects (commercial harvest, nutrient availability, water transparency, and temperature) reversed the relationship between response metrics (size-at-age and population size) by altering intra-specific competition pressure. Likewise, Rossi and Leiner (2022) revealed that density feedback relationships between small mammal population size and growth were affected by fire, intra-specific competition, and additional environmental variables. Additional environmental factors may have a compounding or competing influence on the relationship between response metrics and the underlying mechanisms, interactions, and feedback loops. As such, predicting outcomes of a disturbance on the relationship between body condition and population size is complex.

We found some evidence that disturbance characteristics can influence the relationship between body condition and abundance responses to disturbance. However, the relationships were not robust to sensitivity analyses, highlighting the uncertainty of these links. If they are real effects, the implication is that the underlying mechanisms of disturbances can change intra-specific competition pressure, thereby altering the relationship between abundance and body condition. For example, pulse disturbances (e.g., fire, logging, drought) can greatly reduce resources for some species, which could increase intra-specific competition resulting in both lower body condition and abundance. Pulse disturbances can also result in large direct mortality for some species, which would lower abundance, but body condition may increase due to reduced intra-specific competition between surviving individuals. Under press disturbances, some species are more competitive (e.g., edge specialists, habitat generalists) which could increase carrying capacity, resulting in both higher abundance and body condition. In contrast, under press disturbances such as fragmentation, the abundance of some species may increase within the remaining fragments, thereby increasing intraspecific competition leading to poorer body condition (Ostfeld 1994). It will be important to continue investigating how disturbance characteristics influence important underlying mechanisms that may drive changes in different response metrics and their relationship.

In addition, future research should investigate whether combined abundance and body condition responses can provide better insight into disturbance impacts and extinction risk. For example, if a population has lower abundance and the persisting individuals have low body condition, is that population at a greater risk of ongoing declines compared to a population with low abundance but better body condition? Alternatively, researchers may ask, is poor body condition a symptom of severe population decline and, therefore, too difficult to correlate with population decline until it is too late for conservation intervention?

5 | Conclusion

Our results suggest that changes in body condition in response to disturbance cannot generally be used to predict how species abundance responds to disturbance. As such, we found little support for the risk disturbance hypothesis or population collapse framework. Future research and monitoring programs investigating the impacts of disturbance on body condition should be careful not to infer population-level responses without the relationship being confirmed for their study population. We highlight important ecological pathways between disturbance, predators, competitors, and resources, and their potential to disrupt the relationship between abundance and body condition responses (Figure 3). We encourage further investigation into these key drivers to empirically test and advance ecological theory.

Author Contributions

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Acknowledgements

We acknowledge the various funders who contributed to the underlying datasets used in this research including the Australian Research Council (LP170101134, AD9031596), the Australian Research Grant Scheme (A18615230), Barrick Kanowna, Charles Darwin University, Edith Cowan University, Holsworth Wildlife Research Endowment, Minerals Research Institute of Western Australia, M.J. Murdock Charitable Trust, Australian Goverment's National Environmental Science Program, Northern Australian Environmental Resources Hub, Norilsk Nickel, Northern Territory Department of Lands, Planning and Environment, OMG Cawse Nickel Operations, Parks Victoria, Placer Dome Asia Pacific Kalgoorlie West Operations, and the Threatened Species Recovery Hub. C.R.D. thanks T and L Churches for access to Mooraberrie. We thank the anonymous reviewers for their feedback on an earlier version of this manuscript. Open access publishing facilitated by Charles Darwin University, as part of the Wiley ‐ Charles Darwin University agreement via the Council of Australian University Librarians.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.wdbrv160k.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.