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Dynamic occupancy modelling to determine the status of a Critically Endangered lizard

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Abstract Monitoring of cryptic or threatened species poses challenges for population assessment and conservation, as imperfect detection gives rise to misleading inferences about population status. We used a dynamic occupancy model that explicitly accounted for occupancy, colonization, local extinction and detectability to assess the status of the endemic Critically Endangered Bermuda skink *Plestiodon longirostris*. During 2015–2017, skinks were detected at 13 of 40 surveyed sites in Bermuda, two of which were new records. Ten observation-level and site-specific covariates were used to explore drivers of occupancy, colonization, extinction and detectability. Sites occupied by skinks tended to be islands with rocky coastal habitat and prickly pear cacti; the same variables were also associated with reduced risk of local extinction. The presence of seabirds appeared to encourage colonization, whereas the presence of cats had the opposite effect. The probability of detection was $p = 0.45$, and on average, five surveys were needed to reliably detect the presence of skinks with 95% certainty. However, skinks were unlikely to be detected on sites with cat and rat predators. Dynamic occupancy models can be used to elucidate drivers of occupancy dynamics, which in turn can inform species conservation management. The survey effort needed to determine population changes over time can be derived from estimates of detectability.

Keywords Bermuda skink, conservation, dynamic occupancy modelling, *Plestiodon longirostris*, population monitoring, reptile

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Introduction

Occupancy models have a long history of use in population status assessment and guiding management decisions for threatened species (MacKenzie et al., 2017). Data are collected using either direct or indirect sampling of a species and used to account for imperfect detection and the proportion of sites where the species is actually present. Compared to standard or static occupancy models, dynamic occupancy models can be used to consider changes that may occur over time and space, which can be one of the main sources of error in monitoring studies (Yoccoz et al., 2001; MacKenzie et al., 2002; Royle & Nichols, 2003). Failure to account for imperfect detection can result in sites appearing to be unoccupied that are actually occupied (i.e. false absences), which is common for cryptic species that may go undetected (Yoccoz et al., 2001). Although occupancy alone is a useful state variable, extinction and colonization probabilities estimated over time can also be modelled in relation to site characteristics. These permit testing of hypotheses concerning the drivers of changes in occupancy and allow stronger inferences concerning the mechanisms underpinning occupancy dynamics.

The Bermuda skink *Plestiodon* (=*Eumeces*) *longirostris* is a cryptic species, categorized as Critically Endangered on the IUCN Red List (Cox & Wingate, 2021) and the only endemic extant terrestrial vertebrate on Bermuda (Davenport et al., 2001). Once considered abundant across Bermuda, the population continues to decline because of habitat loss, anthropogenic activities and invasive species. Declines were observed in the early 1900s when it was reported that skinks were rarely seen on the mainland but prevalent on offshore islands, particularly around coastal cliffs (Verrill, 1902). However, concern for the survival of the species only began nearly a century later, when a conservation campaign was undertaken through the Bermuda Zoological Society. Monitoring commenced shortly thereafter, with a focus on the sites with recent sightings, to elucidate population sizes and demographic characteristics (Raine, 1998; Wingate, 1998; Davenport et al., 2001; Glasspool & Outerbridge, 2004). The island-wide skink population was estimated to be 2,300–3,500 individuals, with a suggestion that the true population size could be 5,000 or more given the likelihood of further sites being discovered (Edgar et al., 2010). Determining the current distribution and population status is necessary to inform conservation management.

In this study we used 3 years of presence–absence surveys across Bermuda to model occupancy, colonization, local

extinction and detectability. Inclusion of potential drivers of these parameters as covariates facilitated the identification of key areas for conservation of the species and appropriate management actions.

Study area

Forty locations were surveyed for the presence of skinks across Bermuda (Fig. 1) during 2015–2017. Surveys were undertaken during April–July when skinks are most active (Edgar et al., 2010). Sites were selected based on historical records or were considered to potentially contain skinks based on existing knowledge of habitat preferences, with emphasis on sites that had not been surveyed for > 10 years (Glasspool & Outerbridge, 2004). Locations were isolated islets or islands, or situated at least 100 m apart on the mainland to ensure independence among sites.

Methods

Surveys

The methodology followed that of Davenport et al. (1997), with skinks captured using pitfall traps. As the Bermuda skink has a home range of c. 10 m² (Davenport et al., 1997), traps were placed 5–20 m apart, with 10–72 traps at each site and a greater number of traps at larger sites to increase the chances of capturing skinks. Average trap density was 31 traps per site (0.008 traps/m²; Supplementary Table 1). The traps were opened during 11.00–16.00 and checked hourly to ensure any trapped skinks did not overheat. Skinks were measured, weighed and identified (e.g. Turner et al., 2019) and then released at the point of capture. Each site was surveyed 2–15 times over the 3-year period (depending on weather and site access). To increase chances of detectability, surveys were not conducted during rain or high winds (> 40 km/h).

Statistical analyses

All statistical analyses were undertaken using R 3.3.2 (R Core Team, 2016) with the function colext in the package unmarked (Fiske & Chandler, 2011). Detection and non-detection data and a multi-season occupancy model were used to assess occupancy, colonization, extinction, detectability and probable distribution of P. longirostris across Bermuda. The parameters were ψ = probability of a site being occupied, p = probability of being detected given presence, γ = probability of colonization, and ε = probability of local extinction. Within each year, the four parameters were assumed to be constant, but changes in occupancy were modelled between years and could be a function of covariates (i.e. site-specific habitat features).

Model covariates

Occupancy probabilities may depend on covariates. Five site-specific covariates identified from previous studies (Davenport et al., 1997; Raine, 1998; Wingate, 1998; Glasspool & Outerbridge, 2004) and discussions with experienced ecologists were included in the models (Table 1). These were constant for all visits to a site and thus permit testing hypotheses about drivers of occupancy, colonization and local extinction. Site-specific covariates included the site type (i.e. mainland or island), because anthropogenic disturbance on the mainland (coastal development, coastal and beach activities, and litter (i.e. discarded cans and bottles, which than be lethal) are known to threaten the skinks (Davenport et al., 1997, 2001; Raine, 1998; Wingate, 1998). Habitat type was recorded as the most prevalent habitat type at each site (dense forest or coastal rock and scrub). Nesting seabird colonies and seasonal fruits provide the skinks with food (Davenport et al., 2001; Madeiros, 2005), and therefore the presence of nesting seabirds (white-tailed tropicbird Phaethon lepturus catsbyii, Bermuda petrel Pterodroma cahow) and the prickly pear cactus Opuntia dillenii were included as site-specific covariates. As the number of traps varied between sites, this was included as a covariate.

Five introduced species (kiskadee flycatcher Pitangus sulphuratus, domestic cat Felis catus, yellow-crowned night heron Nyctanassa violacea, Jamaican anole Anolis grahami and black and brown rats Rattus spp.) were used as observation-level covariates as they are associated with known predatory threats. Although additional predators and competitors are present (Anolis leachi, Anolis sagrei, Anolis extremus, domestic chickens Gallus domesticus, and American crows Corvus brachyrhynchos; Wingate, 2011; Stroud et al., 2017), these would have required more exhaustive surveys and therefore we did not collect data on their distribution sufficient for them to be included in the modelling. We visually confirmed the presence or absence of each of the five observation-level covariates during each trapping occasion.

Model selection and averaging

In our first analysis (the null model), we assumed that all four parameters (ψ, γ, ε, p) were constant across sites and surveys. This was denoted by (.) and no covariates were included. We used this model to provide a comparison with the unadjusted (i.e. naïve occupancy) proportion of sites where at least one skink was detected over the 3-year survey period.

In a second analysis, we included covariates (MacKenzie et al., 2002, 2005) for each of the parameters hypothesized to affect occupancy, colonization, extinction or detection probabilities, using a maximum likelihood approach (MacKenzie et al., 2005). All covariates were standardized
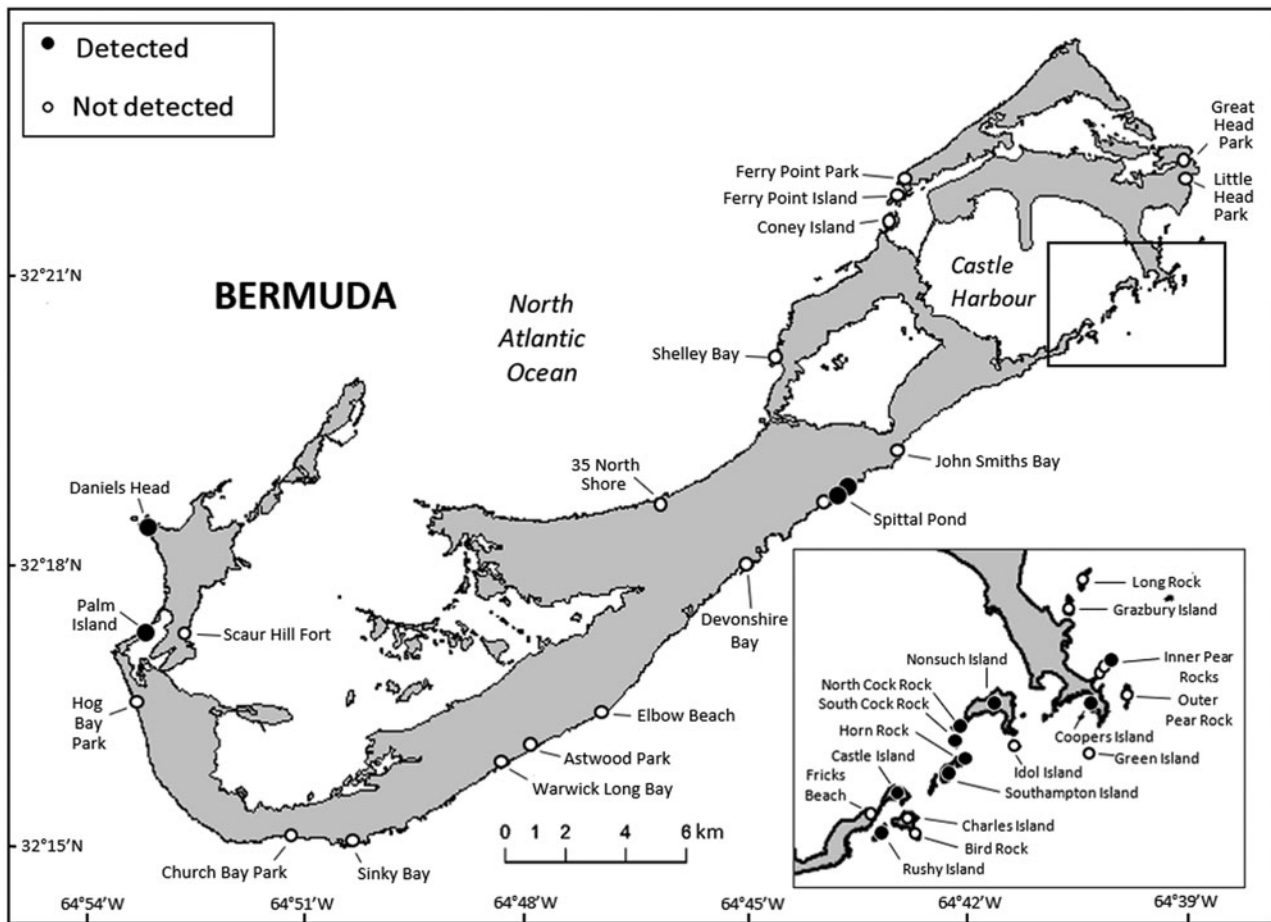
FIG. 1 The 40 localities surveyed for the Bermuda skink *Plestiodon longirostris* during 2015–2017, indicating where it was and was not detected. There were three survey sites at Spittal Pond (Jefferies Hole, Checkboard and East End) and Inner Pear Rocks (Inner, Middle and Outer).

TABLE 1 The five site-specific and five observation-level predictor covariates used in models of site use by the Bermuda skink *Plestiodon longirostris*. All covariates were dichotomous, except for number of traps, which was continuous.

Covariate	Value
Site-specific	
Site type	0 mainland, 1 island
Habitat type	0 forest (dense forest), 1 coastal (rock & scrub)
Seabird nest[1]	0 absent, 1 present
Prickly pear *Opuntia dillenii*	0 absent, 1 present
Number of traps	10–72
Observation-level	
Kiskadee *Pitangus sulphuratus*	0 absent, 1 present
Domestic cat *Felis catus*	0 absent, 1 present
Yellow-crowned night heron *Nyctanassa violacea*	0 absent, 1 present
Anole *Anolis grahami*	0 absent, 1 present
Rats *Rattus* spp.	0 absent, 1 present

[1]White-tailed tropicbird *Phaethon lepturus catsbyii*, Bermuda petrel *Pterodroma cahow*.

(z-score) so that scores could be compared between different types of variable and that the logit scale coefficients ($\hat{\beta}$) were not skewed by unevenly large ranges in the data (MacKenzie et al., 2005). Where logit scale coefficient ($\hat{\beta}$) estimates and associated standard errors (SE($\hat{\beta}$)) are reported, a positive number suggests a positive relationship between the covariate and the model parameter it is a predictor of, and vice versa for negative numbers.

Logit scale coefficient ($\hat{\beta}$) estimates were back-transformed using the *plogis* function in *R* to give the model parameter estimates. Then, using the package *AICcmodavg* in *R*, we assessed the fit of our models using a goodness-of-fit test (MacKenzie–Bailey test) based on bootstrapping (10,000 iterations) and Pearson's χ^2. The level of significance was set at P = 0.05, with larger values indicating a poorer fit (MacKenzie & Bailey, 2004; Wright et al., 2016). To identify the most parsimonious and biologically plausible models for the observed data and assess which combination of covariates best explained the detection histories observed, we calculated and ranked Akaike's information criterion (AIC)

TABLE 2 Ranking of the best fitting models of occupancy (ψ), detection (p), colonization (γ) and extinction (ε) and their covariates, with AIC values, ΔAIC, AIC model weights (w_i), cumulative AIC model weights (cw) and the number of parameters (K) in the top three ranked models of the occupancy of the Bermuda skink.

Model no.	Occupancy model notation[1]	AIC	ΔAIC	w_i	cw	K
1	ψ (PP + ST + HT), γ (PC + SB), ε (HT + PP), p (SB + PR + PP + CC + HT)	168.12	0.00	0.71	0.71	12
2	ψ (SB + PP + ST + HT), γ (PC + ST + SB), ε (HT + PP), p (PR + PP + HT)	171.33	3.21	0.14	0.85	16
3	ψ (.), γ (.), ε (.), p (SB + PR + PP + PC + HT + ST)	173.69	5.57	0.11	0.96	10

[1]PR, presence of rats; PC, presence of cats; HT, habitat type; ST, site type; NT, no. of traps; PP, presence of prickly pear; SB, presence of nesting seabirds.

values for model comparison (Akaike, 1973; Burnham & Anderson, 2002). A set of candidate models was generated by selecting those that had a summed AIC weight of at least 0.95, indicating there was 95% confidence these models best explained the data. If there were multiple top ranked models, a weighted model averaging technique was applied (Burnham & Anderson, 2002) to estimate the detection, occupancy, colonization and local extinction probabilities (with standard errors).

To optimize the survey design, the probability of detecting Bermuda skinks at least once if visiting a site K times was calculated from our best model to determine if the species was truly absent from a site, using the following expression (Pellet & Schmidt, 2005; Barata et al., 2017):

$$K = \frac{\log\left(1 - p^*\right)}{\log\left(1 - p\right)}$$

where p is the detection probability and $p^\star$ is the desired probability of detecting the species at an occupied site on at least one of the K visits, set to 0.80, 0.90, 0.95 and 0.99.

Results

On average, we visited sites five times (range 2–15 visits) over the 3 years. Of the 40 sites surveyed, we confirmed the occurrence of the skink at 13 sites (Supplementary Table 1). The naïve occupancies (calculated as the proportion of sites where presence was confirmed) were 0.25 (8/32) in 2015, 0.48 (12/25) in 2016 and 0.11 (4/38) in 2017. The estimated probability of occupancy using the null model (AIC = 233.91) was 0.22 ± SE 0.08 across the 3 years.

The top three models were selected as they had a cumulative weight of 0.96, indicating these models best explained the data (Table 2). As the goodness-of-fit test had P < 0.05 we accept the hypothesis that the models adequately fit the data (model 1: $\chi^2 = 205.4$, P = 0.02; model 2: $\chi^2 = 187.1$, P = 0.03; model 3: $\chi^2 = 140.5$, P = 0.01). The weighted model averaged estimates of occupancy (ψ), colonization (γ), local extinction (ε) and detection (p) probabilities were taken as the final estimates. The estimate of occupancy (0.25 ± 0.06) did not vary substantially from the naïve estimate because the detection probability was relatively high (0.45 ± SE 0.06), and therefore estimates are reasonably unbiased (MacKenzie et al., 2002; Table 3).

Parameter estimates using the top model (AIC value = 168.12) suggest there was a positive relationship between skink presence and coastal habitat type ($\hat{\beta}$ 2.44 ± SE 0.61), the presence of prickly pear cacti (1.48 ± 0.55) and island sites (1.48 ± 0.55). The presence of cats negatively influenced colonization (−0.32 ± 0.65), whereas the presence of seabirds positively influenced colonization (3.10 ± 0.39). Local extinction was less likely in coastal habitat type (−3.10 ± 0.39) and where prickly pear cacti were present (−3.10 ± 0.39). Detection was positively influenced by the presence of seabirds (7.10 ± 0.21), the coastal habitat type (5.34 ± 0.22) and prickly pear cacti (3.54 ± 0.54), whereas skinks were unlikely to be detected where rats were present (−2.94 ± 0.45) and even less so with cats (−4.30 ± 0.25). As all three of the top models were influenced by the same covariates and in the same directions, this suggests there is considerable support for their inclusion. We found no support for any influence of the presence of kiskadees,

TABLE 3 Transformed parameter ($\hat{\beta}$) estimates for the top three models listed in Table 2, with weighted model averages. All associated standard errors (SE) are included. The first, second and third set of coefficients are for model terms associated with the occupancy (ψ), colonization (γ) and local extinction (ε) parameters, respectively. The fourth set of coefficients explained heterogeneity in detection probabilities (p) associated with different surveys.

Occupancy model notation[1]	ψ ± SE	γ ± SE	ε ± SE	p ± SE
ψ (PP + ST + HT), γ (PC + SB), ε (HT + PP), p (SB + PR + PP + CC + HT)	0.251 ± 0.05	0.128 ± 0.08	0.401 ± 0.08	0.456 ± 0.05
ψ (SB + PP + ST + HT), γ (PC + ST + SB), ε (HT + PP), p (PR + PP + HT)	0.249 ± 0.06	0.350 ± 0.09	0.294 ± 0.07	0.444 ± 0.06
ψ (.), γ (.), ε (.), p (SB + PR + PP + PC + HT + ST)	0.236 ± 0.08	0.132 ± 0.06	0.312 ± 0.07	0.431 ± 0.09
Weighted model averages	0.248 ± 0.06	0.203 ± 0.08	0.351 ± 0.08	0.448 ± 0.06

[1]PR, presence of rats; PC, presence of cats; HT, habitat type; ST, site type; NT, no. of traps; PP, presence of prickly pear; SB, presence of nesting seabirds.

yellow-crowned night herons or anoles, or the number of traps used, on ψ, γ, ε and p.

Minimum number of surveys

To improve the survey design for future monitoring, we calculated the number of surveys required to detect the Bermuda skink at a given site. Assuming skinks are imperfectly detected (detection probability < 1), detection probabilities of 0.80–0.99 were chosen to reflect a high chance of detecting skinks if present. We found that three (mean 2.74) surveys were needed for a 0.80 probability, four (3.92) for a 0.90 probability, five (5.10) for a 0.95 probability and eight (7.85) for a 0.99 probability that the Bermuda skink will be detected at a site.

Discussion

Occupancy probability

Occupancy was related to habitat type, site type and presence of prickly pear cacti. This provides evidence that rocky coastal habitats, particularly on offshore islands, are refuges that support and maintain skink populations (Glasspool & Outerbridge, 2004). Areas with greater levels of habitat degradation and loss (especially on the mainland) were less likely to be occupied than islands (skinks were detected on four mainland sites compared to nine island sites). This suggests that skinks require relatively undisturbed native habitats to thrive, and they could therefore act as important biological indicators of the condition of coastal habitats in Bermuda.

The presence of scrub vegetation and prickly pear cacti may provide a seasonal source of fruit, attract invertebrate prey species, provide shelter and refugia for skinks, and play a key role in erosion control (Le Houérou, 1996). Raine (1998) also noted an association between skinks and areas dominated by coastal vegetation such as sea ox-eye *Borrichia arborescens* and salt grass *Spartina patens* on Inner Pear, Charles Island and Spittal Pond. Therefore, clearing areas of invasive plants such as Brazil pepper *Schinus terebinthifolia* and asparagus fern *Asparagus densiflorus* in suitable coastal locations would be beneficial to skink survival. This would simplify migration between population fragments and increase the probability of population survival.

Although surveys conducted during 1998–2014 did not report occupancy or detectability of the Bermuda skink, our study indicates the species' range is declining, as we found skinks at only 11 of the 26 sites occupied in the previous 20 years, and we detected a skink on more than one sampling occasion at only seven sites. As 67% of detections were in eastern Bermuda (i.e. within the Castle Harbour area), these subpopulations appear to comprise the majority

of the population and would benefit from increased habitat management to control invasive vegetation and reduce the harmful effects of litter (i.e. discarded empty bottles and cans), which can be lethal to the skinks (Jones, 2015).

Colonization and extinction probabilities

Seabirds were found to be important predictors of colonization. This confirms previous suggestions that skinks have a mutualistic relationship with Bermuda's nesting seabirds because skinks opportunistically forage in the seabirds' nests, feeding on failed eggs, carrion such as dead chicks and uneaten fish (Davenport et al., 1997). The installation of artificial nesting burrows has been an important component of the recovery of Bermuda's breeding white-tailed tropicbirds and Bermuda petrels (Madeiros, 2008), so the continuation of this process may help to sustain the skink and encourage its colonization of suitable locations.

However, the probability of colonization by skinks in the presence of cats is low, as cats have been observed predating skinks on many occasions (Garber, 1988). Domestic and feral cats are a global threat to many threatened species (Medina et al., 2011). Bermuda has a high number of domestic and feral cats relative to its size (McGrath, 2014), and a strategy for all aspects of cat management on Bermuda, including the creation of a legislative and regulatory framework, is needed.

Surprisingly, local extinction was not influenced by any predator covariates, but the absence of prickly pear cacti and rocky coastal habitat were key factors. The rocky remains of historical defence fortifications on some islands seem to provide good skink habitat. Changes in habitat are therefore most likely to be important indicators for predicting local extinction of the skink. Mean extinction probabilities tended to be higher than average colonization probabilities. The variability in average colonization and extinction probabilities suggests that the various subpopulations are going through temporal fluctuations in site occupancy.

Detection probability

We assessed the presence of multiple predator species alongside the detection of skinks at each site to determine which species pose threats to remnant skink populations. Although kiskadees, herons and anoles have previously been documented as predators (Davenport et al., 1997), these were not covariates retained in the top models (anoles: AIC > 234.93; herons: AIC > 234.04; kiskadees: AIC > 234.30). Birds are capable of accessing all sites and anole lizards are widespread across Bermuda (Macedonia et al., 2016). However, the recent arrival in 2011 and subsequent establishment of the Cuban brown anole *Anolis sagrei* has been identified as a potential threat to the Bermuda skink

and warrants monitoring (Stroud et al., 2017). The presence of rats and cats was found to negatively affect detection of the skinks. Continued monitoring of the prevalence of predators at each study site would determine the threat level they pose to the skink and whether the management of introduced predators or competitors at a site would facilitate recovery of the skink.

Improving parameter estimates

Precise estimates of occupancy require a large number of sites, but for threatened species there may be insufficient sites for rigorous replication. Because of occasional inclement weather and limited access, many of the sites in this study were visited only twice. Consequently, low precision, with high standard errors of estimates, is likely. To improve the precision of the estimated occupancy rate, increasing the number of surveys to at least five should result in a 0.95 detection probability, but there would be little gain in precision by undertaking more than five surveys.

Conclusion

Bermuda skinks exhibit high variation in occupancy and abundance between years (Turner et al., 2019). The patchy distribution of this species and the high number of threats are constraints on dispersal and recruitment. Our findings demonstrate that the management of the remaining skink populations depends on (1) continuation of control of non-native predators such as cats and rats, and (2) restoring native coastal habitat on offshore islands. The apparently mutually beneficial relationship between skinks and seabirds and how this affects skink occupancy dynamics merits further research. Likewise, the impact on extinction–colonization dynamics of skink mortality in discarded bottles needs elucidation. New initiatives to explore opportunities for restoring populations on undisturbed offshore islands are needed to ensure the survival of the endemic Bermuda skink.

Author contributions Analysis, writing: HT, RAG; experimental and statistical design: HT, RAG; field work: all authors; revision: RAG, GG, MEO.

Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards, was approved by Chester Zoo and the University of Kent Research and Ethics Committee and was conducted under permits issued by the Government of Bermuda's Department of Environment and Natural Resources. Capture and handling of skinks were undertaken in accordance with the conditions of the licence.

References

AKAIKE, H. (1973) Information theory as an extension of the maximum likelihood principle. In *Second International Symposium on Information Theory* (eds B.N. Petrov & F. Csaki), pp. 267–281. Akademiai Kiado, Budapest, Hungary.

BARATA, I.M., GRIFFITHS, R.A. & RIDOUT, M.S. (2017) The power of monitoring: optimizing survey designs to detect occupancy changes in a rare amphibian population. *Scientific Reports*, 7, 16491.

BURNHAM, K.P. & ANDERSON, D.R. (2002) *Model Selection and Multi Model Inference: A Practical Information-Theoretic Approach.* 2nd edition. Springer-Verlag, New York, USA.

COX, N.A. & WINGATE, D.B. (2021) *Plestiodon longirostris*. In *The IUCN Red List of Threatened Species* 2021. dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T8218A121499536.en [accessed 29 November 2021].

DAVENPORT, J., HILLS, J., GLASSPOOL, A. & WARD, J. (1997) *A Study of Populations of the Bermudian Rock Lizard (Skink)*, Eumeces longirostris, *Cope (1861), on the Islands of Nonsuch and Southampton, Bermuda*. Government of Bermuda, Department of Agriculture and Fisheries, Flatts, Bermuda.

DAVENPORT, J., HILLS, J., GLASSPOOL, A. & WARD, J. (2001) Threats to the Critically Endangered endemic Bermudian skink *Eumeces longirostris*. *Oryx*, 35, 332–339.

EDGAR, P., KITSON, L., GLASSPOOL, A. & SARKIS, S. (2010) *Recovery Plan for the Bermuda Skink* Eumeces longirostris. Government of Bermuda, Department of Conservation Services, Flatts, Bermuda.

FISKE, I.J. & CHANDLER, R.B. (2011) *Unmarked*: An *R* package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, 43, 10.

GARBER, S.D. (1988) *Behaviour and Ecology of the Endangered Endemic Bermuda Rock Lizard (*Eumeces longirostris*)*. Rutgers University, New Jersey, USA.

GLASSPOOL, A. & OUTERBRIDGE, M. (2004) *A Population Re-Survey of the Bermuda Skink*, Eumeces longirostris *Cope (1861), on Southampton Island, Castle Harbour*. Bermuda Zoological Society, Flatts, Bermuda.

JONES, S. (2015) Litter a 'death trap' for skinks. *The Royal Gazette*, 2 July 2015. royalgazette.com/environment/news/article/20150702/litter-a-death-trap-for-skinks [accessed 10 February 2022].

LE HOUÉROU, H.N. (1996) The role of cacti (*Opuntia* spp.) in erosion control, land reclamation, rehabilitation and agricultural development in the Mediterranean basin. *Journal of Arid Environments*, 33, 135–159.

MACEDONIA, J.M., CLARK, D.L. & MCINTOSH, A.P. (2016) Differential range expansion and habitat use among the naturalized *Anolis* lizards of Bermuda. *Herpetological Review,* 47, 529–535.

MACKENZIE, D.I. & BAILEY, L.L. (2004) Assessing the fit of site-occupancy models. *The Journal of Agricultural, Biological and Environmental Statistics*, 9, 300–318.

MACKENZIE, D.I., NICHOLS, J.D., LACHMAN, G.B., DROEGE, S., ROYLE, J.A. & LANGTIMM, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248–2255.

MACKENZIE, D.I., NICHOLS, J.D., ROYLE, J.A., POLLOCK, K.H., BAILEY, L.L. & HINES, J.E. (2005) *Occupancy Estimation and Modelling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier Academic Press, Cambridge, USA.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2017) *Occupancy Estimation and Modelling: Inferring Patterns and Dynamics of Species Occurrence.* 2nd edition. Elsevier Academic Press, Cambridge, USA.

Madeiros, J. (2005) *Recovery Plan for the Bermuda Petrel (Cahow)* Pterodroma cahow. Department of Conservation Services, Flatts, Bermuda.

Madeiros, J. (2008) *Breeding Success Survey of White-Tailed Tropicbird* Phaethon lepturus catsbyii *on the Islands of Bermuda – 2006 to 2008 Nesting Seasons and Comparison of Breeding Success Between Natural and Artificial 'Igloo' Nest Sites.* Department of Conservation Services, Flatts, Bermuda.

McGrath, L. (2014) Feral cats a 'serious threat'. *The Royal Gazette*, 22 September 2014. royalgazette.com/other/news/article/20140922/feral-cats-a-serious-threat [accessed 10 Feburary 2022].

Medina, F.M., Bonnaud, E., Vidal, E., Tershey, B.R., Zavaleta, E.S., Donlan, J. et al. (2011) A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology*, 17, 3503–3510.

Pellet, J. & Schmidt, B.R. (2005) Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence. *Biological Conservation*, 123, 27–35.

R Core Team (2016) *R: A Language and Environment for Statistical Computing*. The R Foundation for Statistical Computing, Vienna, Austria.

Raine, A. (1998) *A study of the morphological differentiation, fluctuating asymmetry and the threats facing isolated populations of the Critically Endangered Bermuda rock lizard (*Eumeces longirostris*).* MSc thesis. University College London, London, UK.

Royle, J.A. & Nichols, J.D. (2003) Estimating abundance from repeated presence–absence data or point counts. *Ecology*, 84, 777–790.

Stroud, J.T., Giery, S.T. & Outerbridge, M.E. (2017) Establishment of *Anolis sagrei* on Bermuda represents a novel ecological threat to Critically Endangered Bermuda skinks (*Plestiodon longirostris*). *Biological Invasions*, 19, 1723–1731.

Turner, H., Griffiths, R.A., Outerbridge, M.E. & Garcia, G. (2019) Estimating population parameters for the Critically Endangered Bermuda skink using robust design capture–mark–recapture modelling. *Oryx*, 55, 81–88.

Verrill, A.E. (1902) *The Bermuda Islands*. Connecticut, New Haven, USA.

Wingate, D.B. (2011) The successful elimination of cane toads, *Bufo marinus*, from an island with breeding habitat off Bermuda. *Biological Invasions*, 13, 1487–1492.

Wingate, R.S. (1998) *A comparison of demography and morphological variation in two insular populations of the Bermuda rock lizard (*Eumeces longirostris*).* BSc thesis. University of Wales, Cardiff, Wales.

Wright, W.J., Irvine, K.M. & Rodhouse, T.J. (2016) A goodness-of-fit test for occupancy models with correlated within-season revisits. *Ecology and Evolution*, 6, 5404–5415.

Yoccoz, N.G., Nichols, J.D. & Boulinier, T. (2001) Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution*, 16, 446–453.