

2019-06-30

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<http://hdl.handle.net/10026.1/13333>

10.1111/jzo.12664

Journal of Zoology

Wiley

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1 Morphological divergence and reduced ectoparasite prevalence in an
2 introduced population of a Caribbean anole

3
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7
8 **Abstract**

9 Invasive species are characterized as effective dispersers, allowing them to rapidly colonize an area
10 shortly after being introduced. As biological invasions become increasingly common understanding
11 what factors drive a species' ability to rapidly colonize new habitats will be important for future
12 conservation management. Theoretical models predict that spatial sorting of an invasive population
13 will select for enhanced dispersal-related traits and lower prevalence of parasitic infections of
14 individuals on the vanguard of range expansion when compared to those of the core population. In
15 support of the models, there is a growing body of evidence that demonstrates both features are
16 common in invasive populations, although, these observations stem from mainland systems, over
17 larger spatial scales. Here we investigated the morphology and ectoparasite prevalence of Maynard's
18 anole (*Anolis maynardi*) in its native range Little Cayman, and across its introduced range Cayman
19 Brac where it was discovered 31 years ago. We tested for morphological divergence, ectoparasite
20 prevalence, and the effects of parasite load on body condition between the native population and the
21 core, intermediate and range edge populations within the introduced range. Our results suggest that
22 spatial sorting could have selected for decreased ectoparasite prevalence on the range edge of the
23 introduced population, across an area of just 39 km². However, there was no difference in hind-limb
24 length, the character that is expected to enhance dispersal ability, across the range of the introduced

1 population. Instead, the greatest variation in morphology across the introduced range was found in
2 fore-limb length. Finally, both males and females from the introduced population were of
3 significantly higher body condition than the native population, yet ectoparasite intensity had no
4 effect on the body condition of infested hosts. These results highlight the rapid change of forelimb
5 length and a reduction in parasite prevalence on the range edge of the introduced population, together
6 these attributes have likely contributed to the successful colonization of Cayman Brac by *A.*
7 *maynardi*.

8

9 **Keywords:** *Anolis maynardi*; *Trombiculid* mite; Little Cayman; scaled-mass index; spatial sorting;
10 invasive species.

11

12 **Introduction**

13

14 Rapid spatial expansion into a new range is characteristic of a successful invasive species (Sakai et
15 al., 2001). This behaviour is characterized by dispersal, the non-returning movement of an animal
16 over time that has the potential to generate gene flow across space (Elton, 1958; Ronce, 2007). For
17 invasive populations, natural variation in dispersal ability will determine which individuals drive the
18 range expansion (Phillips, Brown, & Shine, 2010a). Thus, the potential mates for an animal on the
19 vanguard will also be determined by dispersal ability and, if the traits are heritable, their offspring
20 will have similar characteristics (Phillips et al., 2008; Chuang & Peterson, 2016). This spatial
21 selection allows for traits advantageous for dispersal to accumulate on the range edge and can drive
22 an increase in the rate of range expansion (Perkins et al., 2013). Comparatively, in core populations
23 the selection for local adaptation outweighs that for dispersal and the frequency of dispersal related
24 traits decrease (Phillips et al., 2010a; Perkins et al., 2013). Therefore, phenotypic signatures of this

1 process should be evident between core and range edge populations of a species' range expanding
2 through space (i.e. invasive populations).

3

4 Similarly, range expansion of a population can drive negative clines in parasite prevalence on the
5 expanding front due to sub-sampling from core populations, lower transmission rates via reduced
6 density-dependent interactions on the vanguard and the lowered dispersal ability of parasitized hosts
7 from core populations (Torchin et al., 2003; Phillips et al., 2010b). The direct and indirect effects of
8 parasitic infection for a host, such as impaired competitive or anti-predator behaviors, can have
9 detrimental fitness cost for an individual (Hatcher, Dick, & Dunn, 2003; Lin et al., 2014).

10 Consequently, the net-negative effects can then be a limiting factor on population fitness, indeed, the
11 success of many invasive species has been attributed to the loss of parasites (Dunn et al., 2012;
12 Watson, 2013). Lower rates of parasitism among vanguard individuals can allow resources that
13 would otherwise be used for immunity to be re-directed for activities such as movement and
14 foraging, enhancing the fitness of vanguard populations (Phillips et al., 2010b; Chuang and Peterson,
15 2016). The enhanced viability of vanguard populations presents conservation managers tasked with
16 controlling the spread of an invasive population with 'moving targets' and makes predicting the rate
17 and extent of range expansion challenging to forecast (Campbell and Echternacht, 2003; Phillips et
18 al., 2010b)

19

20 These two traits, morphological divergence and loss of parasites, can be thought of as indicators of a
21 dispersal phenotype, because as a population expands its range the selection for these traits is more
22 pronounced on the vanguard (Phillips et al., 2010b; Perkins et al., 2013). There is a growing number
23 of biological invasions where spatial selection for a dispersal phenotype on the expanding front has
24 been demonstrated. Morphological divergence of dispersal-related traits in vanguard populations has
25 been observed in amphibians, for example in Australia with the invasive cane toad (*Rhinella marina*)

1 and in France with the invasive African clawed frog (*Xenopus laevis*) (Phillips et al., 2006; Louppe
2 et al., 2017). Similarly, reduced parasite prevalence in range-edge populations has been demonstrated
3 with the blue striped snapper (*Lutjanus kasmira*) in Hawaii and the common house geckos
4 (*Hemidactylus frenatus*) in Australia. In both cases there is a clear decrease in parasite prevalence
5 moving from core, intermediate, to range-edge populations (Gaither et al., 2013; Coates et al., 2017).
6 In the examples for both, parasite loss and enhancement of dispersal related traits, these processes
7 have mostly been observed within mainland systems at large spatial scales, whether spatial selection
8 results in similar trends on small islands systems in much more confined systems has yet to be
9 investigated.

10

11 In this study we investigated Maynard's Anole (*Anolis maynardi*), an arboreal lizard that is native to
12 Little Cayman, a small island (26 km²) within the Cayman Islands (Garman, 1888). The species was
13 first discovered to be introduced on the nearby island of Cayman Brac (39 km²) in 1987, near the
14 airstrip on the west end of the island (Franz, Morgan, & Davies, 1987). Then, a 2009 survey found
15 the introduced population had become abundant in the central forest area of the island and had
16 diverged from the native population in traits such as tibia and radius length, but morphological
17 differences could not be clearly explained by differences in habitat use (Herrel et al., 2011). The aim
18 of our study was to investigate whether indicators of spatial selection dynamics (i.e. dispersal related
19 traits) could be observed on the range edge of *A. maynardi's* invasion of Cayman Brac. Additionally,
20 we document ectoparasite presence to compare prevalence of ectoparasites between native, core, and
21 range edge populations to see if spatial sorting has resulted in a reduction in parasite prevalence on
22 the range edge. Finally, the impact of ectoparasite infestation on host's body condition was
23 investigated to test if any reduction in parasite load had given the introduced population a fitness
24 advantage. We look at these two traits, morphological differences and parasite prevalence, between
25 core and range edge populations as indicators of spatial sorting within an invasive population and

1 therefore assess whether the process of spatial sorting in a range expanding population can be
2 observed across small spatial scales in an island system.

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6 **Methods**

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8 Field sites

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10 *A. maynardi* were sampled in 2017 in the introduced range Cayman Brac (July 2-16) and in the
11 native range Little Cayman (July 18 -24). Daily sampling was conducted between 8:00 -18:00 at sites
12 in coastal scrublands and dry forest habitats, spaced roughly two kilometers apart. Global positioning
13 coordinates were recorded for every individual (Figure 1) and used to classify individuals according
14 to their capture sites. Individuals were categorized as belonging to these four populations: Little
15 Cayman (Native) and within 6 km (Core), 12 Km (Intermediate), or 18 Km (Range edge) from the
16 introduction point on Cayman Brac. These three sub-populations from Cayman Brac are hereafter
17 referred to as ‘dispersal groups’.

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21 Field data collection

22

23 All individuals were captured by hand or noose. An infrared thermometer was used immediately
24 after to record body temperature, taken on the ventral side of each animal and perch temperature to
25 the nearest 0.1 °C (Rowley & Alford, 2007). For every captured individual the following habitat use

1 characteristics were recorded: perch height, perch diameter and distance to nearest tree > 1 m in
2 height.

3

4 Morphological characteristics were measured using digital calipers to the nearest 0.01 mm and mass
5 was determined by weighing with a digital scale to the nearest 0.01 gram. For each individual the
6 following morphological characteristics were recorded, snout-vent length (SVL), head width, head
7 depth, head length, humerus length, radius length, metacarpal length, longest-toe forelimb, femur
8 length, tibia length, metatarsal length, and longest-toe hindlimb. The sex of each lizard was
9 determined by the presence of secondary sexual characteristics (e.g. post cloacal scales). Only adult
10 lizards were used for analysis, the cut off size for mature females was > 45 mm SVL and for adult
11 males, the presence of enlarged tail base, large dewlap area, and a minimum of > 50 mm SVL was
12 used to determine maturity (Lovern, Holmes, & Wade, 2004). All measurements were taken on the
13 right side of each animal by VB. From these morphological characters three additional variables
14 were calculated: total forelimb length, total hindlimb length and body condition. The scaled-mass
15 index (SMI) was used as an estimate of body condition because this method allows for relative
16 comparisons between populations and sexes that have different mass/length relationships (Peig and
17 Green, 2010). This is accomplished by standardizing to the mean SVL and including a scaling
18 component that accounts for the non-linear relationships between mass and length across
19 populations and sexes (Peig and Green, 2009). The natural logarithm of mass and SVL was used in
20 the formula: $SMI_i = M_i (L_0/L_i)^{bSMA}$, where M_i is the body mass of individual i , L_0 is the mean of
21 SVL for the sample, L_i is the SVL for individual i , $bSMA$ is the scaling exponent calculated by
22 taking the slope of a standardized major axis regression of mass on length, and SMI_i is the
23 standardized body condition of individual i (Peig and Green, 2009). The scaling component was
24 calculated using the 'smatr' R package (Warton & Ormerod, 2007).

25

1 Finally, a hand lens (10x), was used to carefully inspect every individual for ectoparasites presence,
2 which was then used to calculate ectoparasite intensity (the number of mites per host) and
3 ectoparasite prevalence (the number of infested individuals in the population). For the purposes of
4 this study, parasites were identified to the family level as larval *Trombiculidae* spp. and ruled out as
5 larval *Amblyomma torrei*, a known reptile tick found in the Cayman Islands, based on morphological
6 features such as the gnathosoma characteristics, lack of dorsal scutum, and lack of festoons
7 (Whittick, 1939; Shatrov & Kudryashova, 2006).

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10 Statistical analysis

11

12 Prior to analysis, all morphological and habitat use variables were natural log transformed to meet
13 assumptions of normality and homoscedasticity in the linear models. Only males (n = 42) were used
14 in the morphological comparisons between dispersal groups because the small sample size between
15 dispersal groups for females (n = 12) precluded statistical analysis. Size correction for the
16 morphological variables used in the linear models and PCA analysis was done by taking the residuals
17 from a linear regression of each variable against SVL.

18

19 Initial comparisons of morphology between male lizards from each island was done using a principal
20 component analysis (PCA) for all size corrected morphological characters as loading variables
21 except for total forelimb and hindlimb lengths, as they were represented by their individual
22 segments. Next, a series of linear regressions were used to further investigate whether habitat use
23 and morphology differed between native and introduced populations. Separate linear models were
24 used to compare each of the three habitat use variables, the two temperature variables, the overall
25 body size (SVL), and limb lengths for each island.

1

2 To specifically address whether dispersal related traits differed between dispersal groups within the
3 introduced range, separate linear regressions were built for total forelimb and hindlimb length as
4 dependent variables. The explanatory variables included in the models were perch diameter, perch
5 height, distance to nearest perch, and dispersal group as independent variables. Explanatory variables
6 were dropped based on likelihood ratio test until a final simplified model was used for each trait
7 (Crawley, 2007). Quantile Quantile plots were visually inspected to confirm the assumptions of
8 normality and a Levene's test was used to confirm homogeneity of variance for each linear model.

9

10 Variables influencing ectoparasite prevalence were tested using a generalized linear model (GLM)
11 fitted with a binomial distribution and a logistic link function. Next, parasite prevalence was added as
12 the response variable and the following explanatory variables were added : island, sex, habitat type,
13 body condition, and an interaction between body condition and island. In a separate model, the
14 parasite intensity data consisted of non-negative integer counts with a high proportion of zeros and
15 few hosts with high intensities, so to analyze factors predicting parasite intensity per host, a GLM
16 was fitted with a negative binomial distribution, a log link, parasite intensity as the response variable,
17 and the same set of explanatory variables used for the prevalence model.

18

19 For the binomial and negative binomial regressions, explanatory variables were dropped from the
20 final model based on examining null vs. deviance residuals and likelihood ratio tests. Body
21 condition was then compared between each sex from two populations and between males in the
22 dispersal groups from the introduced population using separate linear models.

23

1 All statistical analysis was performed in R version 3.4.1 using the ‘factoextra’, ‘ggplot2’, ‘MASS’,
2 and ‘msme’ packages (Venebles & Ripley, 2002; Wickham, 2009; Hilbe & Robinson, 2014;
3 Kassambara & Mundt, 2016; R Core Team, 2017).

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6 **Results**

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8 Habitat use and morphology between native and introduced populations

9

10 Males from the introduced population were found in habitats with a greater distance to nearest perch
11 ($F_{1/89} = 5.739$, $p = 0.018$), but showed no differences in the other habitat use characteristics: perch
12 height ($F_{1/89} = 2.606$, $p = 0.11$, perch diameter ($F_{1/89} = 0.238$, $p = 0.626$), perch temperature ($F_{1/89} =$
13 1.938 , $p = 0.167$), and body temperature ($F_{1/89} = 1.184$; $p = 0.279$). Males from the coastal shrub
14 habitats used broader perches ($F_{1/89} = 8.099$, $p = 0.005$) that had a greater distance to the nearest
15 tree > 1 meter ($F_{1/89} = 23.312$, $p = < 0.001$), when compared to those in the dry forest but did not
16 differ in perch height ($F_{1/89} = 0.726$, $p = 0.396$). In addition, forelimb and hindlimb lengths did not
17 vary significantly between the two habitat types ($F_{1/89} = 1.164$, $p = 0.283$; $F_{1/89} = 1.164$, $p = 0.283$,
18 respectively).

19

20 Most of the variation (43%) in male *A. maynardi* morphology from each island was explained with
21 similar positive loading values for all variables in PC1 except for tibia and metatarsal, which
22 explained the remaining variation in PC2 (14%) (Table 1). Males from Cayman Brac showed a large
23 variation in morphology around each principal component axis, while males from Little Cayman
24 showed little variation and were mostly nested within the ellipse of the introduced population (Figure
25 2).

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Males from each island (native vs. introduced) were not distinguishable by overall body size (SVL) ($F_{1/89} = 2.103$, $p = 0.141$). For morphometric means and standard errors of each sex for both islands see Appendix I. Forelimb and hindlimb lengths were greater for males from the introduced population when compared to the native one ($F_{1/88} = 64.56$, $p = < 0.001$; $F_{1/88} = 33.27$, $p = < 0.001$, respectively). However, forelimb and hindlimb lengths were not correlated to log distance to nearest tree, which is the only habitat use characteristics that they differed in ($df = 89$, $r = 0.05$, $p = 0.62$; $df = 89$, $r = 0.04$, $p = 0.64$, respectively).

Habitat use and morphology comparisons between dispersal groups within introduced population

Within the introduced population, males from each dispersal group (core, intermediate, and range edge) were found to use the habitat in similar ways, we found no differences in the lizards' perch height ($F_{2/39} = 0.061$, $p = 0.941$), perch diameter ($F_{2/39} = 0.592$, $p = 0.558$), or distance to nearest tree ($F_{2/39} = 0.452$, $p = 0.639$). Similarly, snout-vent-length and hindlimb length did not differ between dispersal groups ($F_{2/39} = 0.352$, $p = 0.705$; $F_{2/38} = 1.496$, $p = 0.237$, respectively). However, forelimb length increased with distance from introduction point ($F_{2/39} = 7.337$, $p = 0.002$) (Figure 3). Perch diameter use explained a significant amount of variation in the hindlimb lengths between dispersal groups and was kept as a covariate in the linear model ($F_{1/38} = 7.472$, $p = 0.009$).

A. maynardi ectoparasite prevalence and intensity between native and introduced populations

1 Ectoparasite prevalence was 30% higher in the native population compared to the introduced
2 population of *A. maynardi* (Table 2). Furthermore, within the introduced population all parasitized
3 animals were found in the core and intermediate dispersal groups, while animals from range edge
4 population were unparasitized (Figure 4). Finally, individual body condition was not a predictor of
5 parasite prevalence or intensity (Table 2). However, lizards from the introduced population had
6 significantly higher body condition than con-specifics from the native range for each sex (Males:
7 $F_{1/89} = 17.677$, $p = < 0.001$; Females: $F_{1/24} = 4.834$, $p = 0.038$; Figure 5).

8

9

10 **Discussion**

11

12 Our data reveals two key findings, firstly, male anoles from the range edge population have
13 significantly longer forelimbs than both conspecifics from the native population and the core
14 introduced group, surprisingly hindlimb length between dispersal groups did not differ (Figure 3).
15 This increase in relative forelimb length towards the range edge is independent of measured
16 differences in the habitat use characteristics. Secondly, both male and female anoles from the
17 introduced population have significantly lower rates of *Trombiculid* mite prevalence and intensity
18 compared to the native population (Table 3; Appendix II). Furthermore, there was a clear reduction
19 in ectoparasite prevalence with distance from core populations and towards the range edge on
20 Cayman Brac where, on the range edge, no lizards were found to be parasitized (Figure 4). The lower
21 ectoparasite prevalence on the range edge supports the hypothesis that spatial sorting for less
22 parasitized individuals on the vanguard could have occurred during the current range expansion of *A.*
23 *maynardi* across Cayman Brac, however the morphological evidence is more tenuous and requires
24 further research.

25

1 Increased forelimb length on the range edge of the introduced population

2

3 Forelimb length show a clear increasing trend between core and range edge populations, however
4 hindlimb length has clearly been linked to dispersal capability in anoles, measured by sprint speeds
5 and jumping capabilities and it did not vary across our dispersal groups (Toro et al., 2004; Irschick et
6 al., 2005). Forelimb and hindlimb function in arboreal environments is more complex than in
7 terrestrial ones so there is the possibility that longer forelimbs could contribute to dispersal ability in
8 arboreal species (Cartmill, 1985). However, this is speculative and further work is necessary to
9 demonstrate if there is any mechanistic link between increased locomotor capabilities and longer
10 forelimbs in complex arboreal environments.

11

12 Why forelimb length has shown greater divergence compared to hindlimb length between dispersal
13 groups is not clear. Differences in relative limb lengths between anole populations are typically
14 linked to adaptive differentiation to new habitats but this was not the case in our study (Losos et al.,
15 1997; Losos et al., 2001). Habitat use was consistent between the native and introduced populations
16 and between the dispersal groups in the introduced range, so therefore did not explain the substantial
17 forelimb length divergence. The lizards' habitat use presented in this study are similar to that of
18 Herrel et al. (2011), where distance to the nearest perch differed between the native and introduced
19 population but did not clearly explain any of the differences in relative limb lengths. This implies
20 that the morphological divergence observed in the introduced population is not a result of habitat use
21 differences and that other mechanisms are driving the morphological variation observed.

22

23 Whether longer forelimbs are a heritable trait or not will be important for determining a mechanism
24 for the variation seen in the introduced population. Genetic input from multiple source populations
25 with varying phenotypes can drive morphological divergence of an introduced population, as seen in

1 the large-scale range expansion of *A. sagrei* across Florida (Kolbe, Larson, & Losos, 2007). In
2 contrast, the introduction of *A. maynardi* is rather simple, it has a single source population and has
3 expanded through a relatively homogeneous landscape of dry forest and coastal scrublands (Herrel et
4 al., 2011). Although multiple introductions of *A. maynardi* to Cayman Brac cannot be ruled out, the
5 single source population does not appear to have the variation in limb lengths seen across males from
6 the introduced population (Figure 3). Alternatively, anolis lizards raised in differing structural
7 habitats (e.g. different perch widths) have been shown to exhibit substantial phenotypic plasticity in
8 limb and toepad characteristics (Losos et al., 2000; Losos & Kolbe, 2005). Slight variation in habitat
9 structure across the island could result in the plastic response in limb length growth. Future genetic
10 comparisons of the two populations and common garden experiments will be necessary to rule out
11 that the morphological divergence seen in the introduced population is not a result of founder effects
12 of phenotypic plasticity.

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17 Reduced parasite prevalence on the range edge of the introduced population

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19 Our results support that the reduction of parasites prevalence is a common feature of non-native
20 populations on their range edges (Torchin et al., 2003; Phillips et al., 2010b). What is not always
21 clear is how or if reduced ectoparasite prevalence contributes to the success of an introduced species
22 (Colautti et al., 2004; Prenter et al., 2004). In the case of *A. maynardi*, mite infestation had a
23 negligible effect on body condition (Table 2), other studies have also highlighted an asymptomatic
24 effect of ectoparasites in a range of reptile species based on body condition indices (Conover et al.,
25 2015; Mayer et al., 2015; Barnett et al., 2018). However, body condition indices can only detect

1 major differences in energy reserves between infested and non-infested individuals (Peig & Green,
2 2009). Parasites have been shown to effect reptiles in less obvious ways such as, reducing the quality
3 of sexual displays (Cook, Murphy, & Johnson, 2013), negatively impacting movement and home
4 range size (Main & Bull, 2000), and enhancing immunocompetence (Spence et al., 2017) which all
5 affect the success of invading individuals or populations in complex ways. More detailed measures
6 of host fitness are needed to assess whether the reduced parasite prevalence has benefited *A.*
7 *maynardi* in its introduced range.

8
9 Furthermore, *A. maynardi* is host to five species of nematode, although, endoparasite prevalence was
10 not investigated in this study, it is possible that a combined reduction in the prevalence of all
11 parasites could better explain differences in host body condition (Goldberg & Bursey, 1996; Johnson
12 & Hoverman, 2012). Nematodes found in vital organs can cause direct mechanical damage and thus
13 have direct impact on host health, as seen in cane toads (*R. marina*) in Australia, where infection by a
14 lung nematode directly impacted growth rates across all life stages, likely causing long-term fitness
15 consequences (Kelehear, Brown, & Shine, 2011). Future research should investigate what role, if
16 any, endoparasite infection has in the successful establishment of *A. maynardi* in Cayman Brac.

17
18 Despite ectoparasite prevalence or intensity having no effect on body condition, animals from both
19 sexes had a higher body condition in the introduced range. The differences in condition could
20 potentially be the combined effect of parasite loss, reduced competition, and ecological release into a
21 previously unoccupied arboreal niche across Cayman Brac which would provide access to more
22 resources and positively impact individual body condition (Colautti et al., 2004; Dlugosch et al.,
23 2015). Having larger energy stores is beneficial on the invasion front as it can assist with finding
24 mates in low density situations and counteract costs associated with dispersal (Bonte et al., 2012).

1 Together the increased body condition and reduced parasite load are likely factors that have
2 contributed to the successful colonization of Cayman Brac by *A. maynardi*.

3

4 **Conclusion**

5

6 The results highlight substantial variation in forelimb length, and the overall morphology, of male
7 lizards within the introduced population of *A. maynardi*. . More importantly these differences may
8 have evolved over only 30 years since its first introduction in 1987 in an island only 38 km².

9 Furthermore, *Trombiculid* mite prevalence was dramatically reduced in the introduced population
10 and no infested individuals were found on the invasion range edge. . It is unknown whether the mites
11 found on both islands are the same species, was co-introduced, or invasive to both islands, as they
12 were morphologically indistinguishable and there are no taxonomic records for a *Trombiculid spp.* in
13 the Cayman Islands (Hounscome, 1994).

14

15 Hereby we present information that documents *A. maynardi*'s expanded range and morphological
16 variation across Cayman Brac and the first investigation into ectoparasites affecting the species. The
17 mechanisms for the increased forelimb length observed in the introduced population are not clear and
18 future research is needed, including genetic testing, common-garden experiments, and additional
19 female samples, to explain why the introduced population exhibits a substantially wider variation in
20 forelimb length and overall morphology than found in the native population. Typically observed in
21 mainland invasions, spatial selection dynamics have been shown in this study to select for a reduced
22 ectoparasite prevalence in a small island system where it can positively influence the establishment
23 and viability of an introduced species.

24

25 **Acknowledgments**

1 We would like to thank the Department of Environment of the Cayman Islands for granting the
2 research permit. Additionally, many thanks to Miguel Franco, Caroline Palmer, and the two
3 anonymous reviewers for helpful comments that enhanced the final version of this manuscript.
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6

7 **Conflicts of Interest**

8 There are no conflicts of interest.
9

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 11

Tables and legends

12 **Table 1.** Loadings of the morphological variables in the PCA and the Eigenvalue of each component.

Characters	PC1	PC2
Head depth	0.371	-0.132
Head width	0.285	-0.222
Head length	0.343	-0.356
Humerus	0.291	0.151
Radius	0.368	-0.148
Metacarpus	0.296	0.117
Metacarpus IV	0.311	0.024
Femur	0.336	0.236
Tibia	0.183	0.599

Metatarsal	0.115	0.554
Metatarsal IV	0.310	-0.160
Eigenvalue	2.171	1.252
% variance explained	0.429	0.142

1 **Table 2.** Regression results from the GLMs for (a) parasite prevalence with a binomial distribution, a
2 logistic link function, and 113 degrees of freedom and (b) parasite load with a negative binomial
3 distribution, a logarithmic link function, and 113 degrees of freedom. For all chi- squared test the
4 degrees of freedom is equal to 1. The parameter variable in brackets represents the factor used to test
5 against the null intercept. Bold p-values represent significance

Model	Variable	Coefficients				Chi-squared	
		Estimate	2.5 % CI	97.5 % CI	P- value	χ^2	P-value
(a)	Island (LC)	1.658	0.621	4.899	0.003	16.571	< 0.001
Parasite prevalence	Sex (Males)	1.811	0.012	3.757	0.055	1.085	0.297
	Body condition	-2.577	- 5.721	0.409	0.096	2.854	0.091
(b)	Island (LC)	2.186	0.924	3.541	< 0.001	10.076	0.001
Parasite intensity	Habitat (Forest)	1.082	0.066	2.176	0.034	3.856	0.049
	Body condition	1.179	- 1.479	3.771	0.264	0.786	0.375

Figure legends

- 1 **Figure 1.** Study area with location of animals used in this study as filled circles.

1 **Figure 2.** Male *A. maynardi* points in morphological space of PC1 and PC2 for each population.
2 Loadings and importance of each principal component is listed in table 2. Around each population's
3 data points is a 95% confidence ellipse.

4 **Figure 3.** Total limb length (residuals) for male *A. maynardi* for the native population: LC (N = 49),
5 and each of the three dispersal groups from Cayman Brac: CB (6 Km) as the core population (N =
6 11), CB (12 Km) as the intermediate population (N = 16), and CB (18 Km) as the range edge
7 population (N = 15). Pairwise ANOVA comparisons are presented for the groups within the Cayman
8 Brac population. The asterisks represent significance values of: '****' $p \leq 0.001$; '**' $p \leq 0.01$; '*' p
9 ≤ 0.05 ; 'ns' $p > 0.05$.

10

11 **Figure 4.** Prevalence of *Trombiculid* mite infestation in *A. maynardi* for the native Little Cayman
12 population (LC) and each of the three dispersal groups on Cayman Brac, CB (6 Km) as the core; CB
13 (12 Km) as the intermediate; and CB (18 Km) as the range edge, sample sizes: N = 64, 15, 23, and
14 16, respectively. For each population standard error bars around total prevalence are presented.

15 **Figure 5.** Estimates of body condition (scaled-mass index) for male and female *A. maynardi* from
16 Little Cayman (native range) and Cayman Brac (introduced range).

17

Supplementary material

Appendix I. Morphometric characterization of native (Little Cayman) and introduced (Cayman Brac) populations of *Anolis maynardi*.

Character	Little Cayman		Cayman Brac	
	Males (n = 49)	Females (n = 14)	Males (n = 42)	Females (n = 12)
SVL (mm)	64.9 ± 0.67	49.0 ± 0.39	66.4 ± 0.79	49.3 ± 0.62
Weight (g)	5.9 ± 0.20	2.9 ± 0.09	7.1 ± 0.23	3.2 ± 0.09
Head length (mm)	21.3 ± 0.27	14.5 ± 0.19	22.9 ± 0.34	15.3 ± 0.32
Head width (mm)	9.3 ± 0.12	6.9 ± 0.06	9.8 ± 0.14	7.2 ± 0.09
Head depth (mm)	6.7 ± 0.07	5.2 ± 0.09	7.6 ± 0.10	5.7 ± 0.09
Humerus (mm)	9.9 ± 0.10	7.6 ± 0.10	10.8 ± 0.15	7.9 ± 0.08
Radius (mm)	8.1 ± 0.08	5.9 ± 0.08	8.8 ± 0.10	6.3 ± 0.21
Metacarpal (mm)	2.6 ± 0.03	2.0 ± 0.06	3.1 ± 0.06	2.4 ± 0.15
Longest toe forelimb (mm)	5.4 ± 0.05	3.9 ± 0.09	5.9 ± 0.08	4.2 ± 0.13
Forelimb (mm)	26.1 ± 0.22	19.5 ± 0.23	28.7 ± 0.31	21.0 ± 0.32
Femur (mm)	12.3 ± 0.10	9.3 ± 0.09	13.1 ± 0.14	9.6 ± 0.14
Tibia (mm)	13.2 ± 0.09	10.0 ± 0.06	13.7 ± 0.17	9.9 ± 0.21
Metatarsal (mm)	7.8 ± 0.06	5.9 ± 0.09	8.1 ± 0.10	5.7 ± 0.17
Longest-toe hindlimb (mm)	9.7 ± 0.10	6.9 ± 0.09	10.5 ± 0.13	7.4 ± 0.14
Hindlimb (mm)	42.9 ± 0.30	32.2 ± 0.20	45.4 ± 0.42	32.7 ± 0.41

Table entries are means ± standard errors.

Appendix II. Characterization of parasitism by *Trombiculid spp.* on the native and introduced populations of *A. maynardi*. Lower and upper 95% confidence intervals (CI) for prevalence was calculated using the Wilson's score interval.

Island	Sex	n	Prevalence (%) ¹	2.5 % CI	97.5 % CI	Mean intensity ²
Little Cayman	Male	49	43	30	56.7	4.8
	Female	14	35	16.3	61.2	8
Cayman Brac	Male	42	12	5.2	25.1	4.6
	Female	12	0	0	0	0

¹Number of infested individuals / number of individuals sampled.

²Mean intensity of ectoparasites per infested host.