

# Do differences in bite force and head morphology between a native and an introduced species of anole influence the outcome of species interactions?

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Species invasions may drive native species to extinction. Yet, the role of competition with a closely related native species in the establishment success of an invasive species remains poorly understood. Indeed, opportunities to study native–invasive competition in action are rare, especially at the very first stages of the invasion. We studied the recent invasion of the lizard *Anolis cristatellus* in Dominica, where the native *Anolis oculatus* occurs. We examined the species difference in bite force as a proxy for fighting ability and access to food resources, and its effect on the establishment success of the invasive species. We measured head morphology and bite force of 371 and 129 adults of both species, and compared four allopatric and five sympatric populations in banana farms in an area (Calibishie) where the two species have been in contact for only a few years. This study revealed higher absolute bite forces of *A. oculatus*, ruling out the superior fighting ability hypothesis as a determinant for the establishment of *A. cristatellus* in Calibishie. The species differences in bite force and head morphology are present in allopatry and sympatry, suggesting that recent interspecific competition has no observable effect on these traits. We discuss other possible mechanisms allowing the establishment success of *A. cristatellus* in Dominica.

ADDITIONAL KEYWORDS: agonistic encounters – *Anolis cristatellus* – *Anolis oculatus* – bite force – diet – Dominica – exploitative competition – fighting ability – invasion success – lizard.

## INTRODUCTION

Invasive species can profoundly impact ecosystems, may drive species to extinction and cause economic damage, so much that they have become a prime societal concern (Pimm & Sjoepajd, 1987). Consequently, understanding how invasive species successfully establish and persist in new environments is of paramount importance. The outcome of interactions between native and invasive species may be instrumental in the establishment process of an invasive species (Duyck *et al.*, 2004; Rehage *et al.*, 2005; Blight *et al.*, 2010; Shochat *et al.*, 2010; Engel & Tollrian, 2012; Beest *et al.*, 2013).

Closely related native and invasive species often share ecological niches (Violle *et al.*, 2011), enhancing the importance of resource use and interference competition for the outcome of the invasion process (Holway, 1999; Mooney & Cleland, 2001). When the competition is indirect (exploitative competition), dominance for food (e.g. in geckos: Petren & Case, 1996; and ants: Human & Gordon, 1996; Holway, 1999) and space use (e.g. mussel: Carlton *et al.*, 1999) are among the main factors affecting invasion success. Alternatively, when competition is direct and involves agonistic encounters between native and invasive species, the species with greater fighting ability is expected to dominate the interspecific encounter (Holway & Suarez, 1999; Lailvaux *et al.*, 2004).

Differences in resource use and fighting ability between species may reflect initial (allopatric)

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differences or may alternatively result from the interspecific competition. While ecological character displacement enhances species divergence in sympatry to minimize resource use overlap (Brown & Wilson, 1956; Grant, 1972; Schluter, 2000), an arms race (Parker, 1983) increases interference competitive ability in sympatry (Gill, 1994). Exploitative and interference competitions have mostly been studied separately (but see Holway, 1999) and little is known about their relative effects on species divergence and their consequences for the outcome of competition between native and invasive species.

Bite force is a good candidate to consider regarding these two aspects of competition as this trait is linked to diet and fighting ability in many vertebrates including lizards (Herrel *et al.*, 2001b; Lailvaux & Irschick, 2007), birds (Herrel *et al.*, 2005) and mammals (Santana *et al.*, 2010). Indeed, bite force is a good proxy for fighting ability as it has been linked to male dominance in intraspecific encounters (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Husak *et al.*, 2006; Lailvaux & Irschick, 2007). Moreover, bite force is directly relevant to diet because a greater bite force enables exploitation of larger prey (Herrel & O'Reilly, 2006), more plant matter (Herrel *et al.*, 2004a, b, 2008; Herrel & De Vree, 2009) or more hard-bodied prey (Herrel *et al.*, 1999, 2001b, 2006; Verwajen *et al.*, 2009). In addition, species differences in bite force may impact interspecific competition (e.g. Downes & Bauwens, 2002; Herrel *et al.*, 2004b; see Discussion), although not

all tests have supported this hypothesis (Langkilde & Shine, 2007; Edwards & Lailvaux, 2013). Finally, previous studies have suggested that greater bite forces are associated with a larger head and greater body size (Herrel *et al.*, 2001b; Lailvaux *et al.*, 2004; Husak *et al.*, 2006; Henningsen & Irschick, 2012; Bush *et al.*, 2016), and head morphology may be directly impacted by exploitative competition for food (Adams & Rohlf, 2000; Grant & Grant, 2014) and interference competition through agonistic encounters (Adams, 2004).

This study aims to determine the effect of differences in bite force and head morphology between species on species interactions during the rapid invasion of the Puerto-Rican lizard *Anolis cristatellus* on the island of Dominica, where a closely related native species – *Anolis oculatus* – occurs. *Anolis cristatellus* reached the north-eastern part of Dominica (Calibishie) in 2014 where the two species co-occur in sympatry and potentially compete for space and food resources, resulting in divergence in microhabitat use in sympatry (Dufour *et al.*, 2017). Moreover, several direct agonistic interactions involving fighting and biting have been observed in Calibishie (Fig. 1; C. M. S. Dufour, pers. observ.; 57% of direct male–male fights observed in the field were interspecific) and might drive the shift in behavioural displays observed in *A. cristatellus* in sympatry (Dufour *et al.*, 2018). Finally, because the spread of *A. cristatellus* has been patchy (due to the random spread of this species along the main road), allopatric populations of both species also occur



**Figure 1.** Fighting encounter between *Anolis oculatus* (upper left) and *Anolis cristatellus* (bottom right) males in Calibishie (Dominica). Photography source credit: Claire M. S. Dufour.

throughout Calibishie. The allopatric populations of the invasive species may be the result of the extinction of the native species or may result from establishment of the invasive species in naturally unoccupied sites.

Morphological (head and body size) and performance (bite force) traits were measured in adult *A. cristatellus* and *A. oculatus* in Calibishie in 2016. First, we tested whether head morphology and bite force are correlated in both species. Second, to test if differences in bite force and head morphology may explain the invasion success of *A. cristatellus*, we compared the two species in allopatry and in sympatry. To minimize the possible effect of ecological factors on bite force and head morphology, the two species were sampled in the same habitat type (banana farms; Dufour *et al.*, 2018).

Specifically, the three following predictions were tested:

- 1) Head morphology and body size are positively correlated with bite force in both species.
- 2) Better fighting ability and low overlap in food resource use may favour an invasive species compared to the native species already present. If species interference (i.e. agonistic encounters) is the main determinant of the invasion success, *A. cristatellus* is expected to have a larger head and greater absolute bite force compared to *A. oculatus* in sympatry. Alternatively, if diet segregation is the main factor for the establishment of the invasive species, *A. cristatellus* is expected to be different in head morphology and bite force (higher or lower) compared to the native species in sympatry.
- 3) If fighting abilities have evolved as a result of interference competition, bite force (relative size-corrected or absolute) and head size should increase for both species in sympatry compared to allopatry. Alternatively, if diet has evolved as a result of exploitative competition, bite force and head size should diverge between the species in sympatry compared to allopatry because the species would be adapting to eat different prey.

## MATERIAL AND METHODS

### STUDY SITES AND SAMPLING

From 1 May to 9 June 2016, a total of 371 adult lizards (*A. cristatellus* and *A. oculatus winstoni*, hereafter *A. oculatus*) were sampled in banana farm habitats within the Calibishie region in Dominica across four allopatric sites (two for each species) and five sites where the species were sympatric. According to information from residents, *A. cristatellus* arrived in this region no earlier than 2014 (for more details

see Dufour *et al.*, 2017). Lizards were captured by noose or by hand. To prevent the risk of re-sampling, individual lizards were marked with a non-toxic marker upon release and each population was studied on three to five consecutive days only. Each sampled individual was released at its capture point within 10 h.

### MORPHOMETRICS

Morphological traits [snout–vent length (SVL), head width, head length, head height, lower jaw length, jaw out-lever and snout length, see Herrel & Holanova (2008) for more details] were measured for 215 adult *A. oculatus* (146 males, 69 females) and 156 adult *A. cristatellus* (81 males, 75 females), using a digital caliper ( $\pm 0.01$  mm; model CD-15DC; Mitutoyo, UK) and body mass was measured with an electronic balance ( $\pm 0.01$  g; model FX-3200; A&D, Japan; Supporting Information, Table S1).

### BITE FORCE MEASUREMENTS

*In vivo* bite forces were measured using an isometric Kistler force transducer (type 9203, Kistler Inc., Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5058 A, Kistler Inc., for more details, see Herrel *et al.*, 1999). The place of application of bite forces and gape angle were standardized. Bite forces were measured for 76 adult *A. oculatus* (61 males, 15 females) and 53 adult *A. cristatellus* (35 males, 18 females). Measurements were repeated five times for each animal. The maximum value recorded across the five recording sessions was considered to be the maximal bite force for that animal. Raw values were corrected for the lever arms of the set-up to obtain bite forces in newtons (Table S1). All animals were tested within 5 h after capture.

### STATISTICAL ANALYSES

All statistical analyses were conducted using R-v3 (R Development Core Team, 2011). Separate analyses were performed for males and females given the known dimorphism in head size and shape and bite force in *Anolis* lizards (Herrel *et al.*, 2007). For males and females separately, a principal component analysis (PCA) was performed on the morphological traits measured. The first PC axis, which had an eigenvalue greater than one and describes head size and SVL (Table S2), was retained for further analysis.

First, to test for the correlation between head morphology and bite force, a Pearson's correlation test was performed on the first PC axis (morphology) and the log-transformed bite forces for each species and sex

separately. Second, to test for species divergence in head/body morphology (PC1), and absolute (log-transformed) and relative (residuals of the linear regression between bite force and SVL) bite force, linear mixed-effect models (lme function; Laird & Ware, 1982; Pinheiro *et al.*, 2018) were run with the species, context and the two-way interaction as factors and the population as a random effect. Normality and heteroscedasticity of distributions were checked by plotting the model's residuals. The final (best-fitted) model was selected based on Akaike's information criterion ( $\Delta$ AICc and weight, relative likelihood of a model to be the best among the set of models tested; Burnham & Anderson, 2002).

## RESULTS

### PCA ON HEAD MORPHOLOGY AND SVL

The first PC axis explained 83.6% of the total variance in morphology for males and 88.8% for females. Head dimensions and SVL loaded strongly on the first axis for both sexes (Table S2).

### CORRELATION BETWEEN SVL–HEAD MORPHOLOGY AND BITE FORCE

The first PC axis (representing head morphology and SVL) was significantly and positively correlated to the log-transformed bite forces for males and females of both species (Table 1). Larger lizards (SVL and head) had a greater bite force.

### SPECIES DIFFERENCE IN HEAD MORPHOLOGY AND SVL

Overall, *A. oculatus* had greater head dimensions and body size (SVL) compared to *A. cristatellus* for both sexes, irrespective of allopatry and sympatry (Table 2, Fig. 2).

### SPECIES DIFFERENCE IN BITE FORCE

Overall, *A. oculatus* had greater absolute bite forces compared to *A. cristatellus* for both sexes, irrespective

of allopatry or sympatry (Table 2, Fig. 3). The difference between species was especially striking for females with female *A. oculatus* having a much greater absolute bite force than female *A. cristatellus*.

*Anolis cristatellus* males had a greater relative bite force (size-corrected) than males of *A. oculatus*. There were no significant differences in the relative bite forces between the species for females (Table 2, Fig. 3).

## DISCUSSION

Competition between native and invasive species may be a crucial determinant of invasion success (Duyck *et al.*, 2004; Rehage *et al.*, 2005; Blight *et al.*, 2010; Shochat *et al.*, 2010; Engel & Tollrian, 2012; Beest *et al.*, 2013). Yet, the interaction between native and invasive species is rarely tracked at the beginning of the invasion (Puth & Post, 2005). The present study reveals that the native *A. oculatus* has a larger head and greater absolute bite force compared to the recently introduced *A. cristatellus* in Calibishie, Dominica. Based on these results, the native species is expected to prevail in fights with the invasive species, a prediction supported by field observations of *A. oculatus* chasing *A. cristatellus* (Dufour *et al.*, 2017, 2018). Relative bite force, by contrast, is greater in *A. cristatellus* males than in *A. oculatus* males and did not differ between the species for females, suggesting that different morphological factors might determine the relative bite force between species and sexes. Finally, the differences in the species in absolute and relative bite force and head morphology are maintained in the two contexts, which suggests that interspecific competition has not resulted in the evolution of differences in head morphology or bite force. Nonetheless, the relative role of species interference and exploitative competition between the two species in the evolution of fighting ability and diet requires further study. We discuss (1) the proximate factors of head morphology and bite force species differences, (2) the potential effect of interspecific competition on these traits and (3) the factors that may explain the invasion success of *A. cristatellus* in Calibishie.

**Table 1.** Statistical results from the Pearson's correlation tests between the first PCA axis – representing SVL and head morphological traits – and the log-transformed bite forces according to species and sex

	Males				Females			
	d.f.	<i>t</i>	<i>P</i>	Correlation	d.f.	<i>t</i>	<i>P</i>	Correlation
<i>Anolis oculatus</i>	59	8.702	<0.001	0.749	13	2.655	0.020	0.593
<i>Anolis cristatellus</i>	33	6.149	<0.001	0.731	16	3.195	0.006	0.624

**Table 2.** Statistical results from the final linear mixed-effect models testing the first PC axis on head morphological traits and SVL as well as the absolute and relative bite force according to the species and the context. The model selected (“final model” presented in the table) was the one with the lowest AICc by two units. When the global model (the two factors and the interaction tested) and the model without the interaction did not differ in their AICc by two units, we selected the simplest one (without interaction). Bold P-values highlight significant effects of the fixed variable.

	Males final model AICc = 985, weight = 0.54 (global model AICc = 985, weight = 0.46)					Females final model AICc = 447, weight = 0.52 (global model AICc = 447, weight = 0.48)				
PC1 Head morphology	Value	SE	d.f.	t	P	Value	SE	d.f.	t	P
(Intercept)	1.574	0.433	217	3.635	< 0.001	1.953	0.234	134	8.328	< 0.001
context	0.355	0.515	7	0.690	0.495	0.336	0.284	7	185	0.275
<b>species</b>	<b>-2.654</b>	<b>0.344</b>	<b>217</b>	<b>-7.713</b>	<b>&lt; 0.001</b>	<b>-4.483</b>	<b>0.217</b>	<b>134</b>	<b>-20.687</b>	<b>&lt; 0.001</b>
random				7.249*	0.007				1.282*	0.258
	Males final model AICc = 40, weight = 0.88 (global model AICc = 44, weight = 0.12)					Females final model AICc = 25, weight = 0.80 (global model AICc = 28, weight = 0.20)				
Log (bite force) absolute	Value	SE	d.f.	t	P	Value	SE	d.f.	t	P
(Intercept)	3.056	0.055	87	55.181	< 0.001	1.523	0.191	28	7.988	< 0.001
context	-0.055	0.059	6	-0.930	0.388	0.061	0.253	2	0.243	0.831
<b>species</b>	<b>0.121</b>	<b>0.058</b>	<b>87</b>	<b>2.076</b>	<b>0.041</b>	<b>0.818</b>	<b>0.135</b>	<b>28</b>	<b>6.044</b>	<b>&lt; 0.001</b>
random				1.491e-08*	0.999				2.618*	0.106
	Males final model AICc = 521, weight = 0.27 (global model AICc = 519, weight = 0.73)					Females final model AICc = 150, weight = 0.39 (global model AICc = 150, weight = 0.61)				
Bite force relative to size	Value	SE	d.f.	t	P	Value	SE	d.f.	t	P
(Intercept)	2.757	1.304	87	2.114	0.037	-0.829	1.122	28	-0.738	0.466
context	-0.060	1.695	6	-0.036	0.973	1.758	1.420	2	1.238	0.341
<b>species</b>	<b>-4.030</b>	<b>0.952</b>	<b>87</b>	<b>-4.235</b>	<b>&lt; 0.001</b>	<b>-0.029</b>	<b>1.019</b>	<b>28</b>	<b>-0.028</b>	<b>0.978</b>
random				11.435*	< 0.001				0.452*	0.501

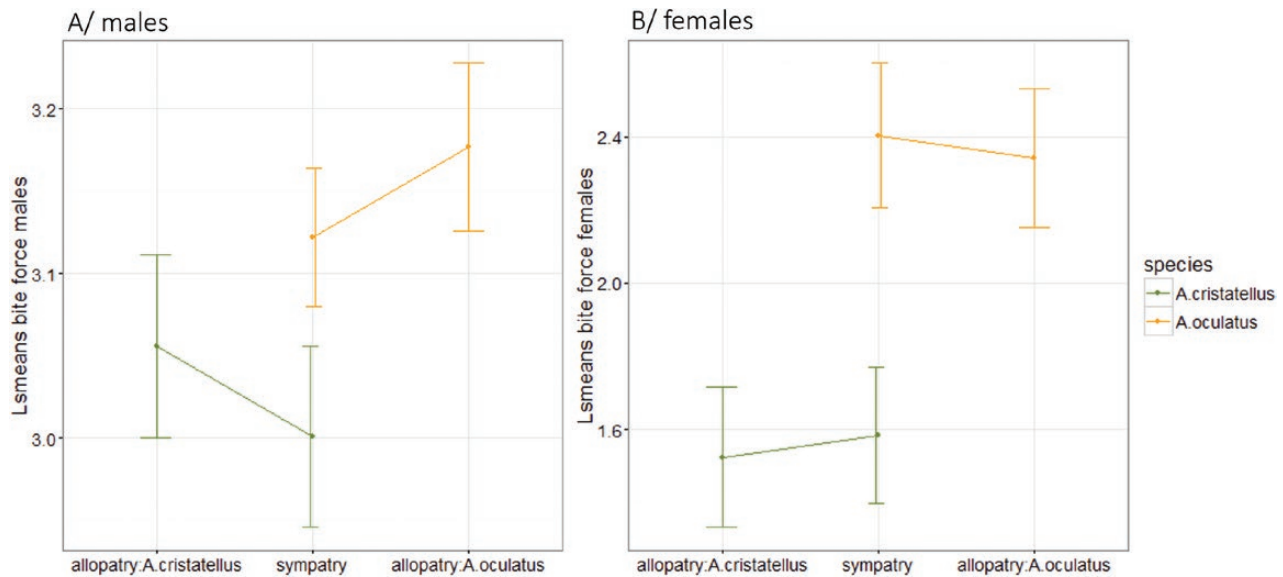
\*Likelihood ratio.

*What are the proximate determinants of the difference in head morphology and bite force?*

The greater absolute bite force of the native *A. oculatus* (compared to the invasive *A. cristatellus*) irrespective of the context suggests the presence of different selective pressures in Dominica vs. Puerto Rico (the native range of *A. cristatellus*).

One potential driver of the bite force and head size differences observed between the two species might be diet (Herrel *et al.*, 2001b; Herrel & O’Reilly, 2006; Herrel & Holanova, 2008). In other lizards, a larger head and greater bite force enable the inclusion of larger prey (Herrel & O’Reilly, 2006), more plant matter (Herrel *et al.*, 2004a, b, 2008; Herrel & De Vree, 2009) or hard-bodied prey items into the diet (Herrel *et al.*, 1999, 2001b, 2006; Verwajen *et al.*, 2009). However, a careful review of the literature reveals similar diets in terms of the proportion of hard vs. soft

prey consumption between *A. cristatellus* from Puerto Rico and *A. oculatus* in Dominica (Wolcott, 1924; Andrews, 1979; Bullock *et al.*, 1993). In a detailed analysis of the stomach contents of 100 *A. cristatellus* from Puerto Rico, Wolcott (1924) revealed that hard prey (Hymenoptera – among which 97% were ants – and Coleoptera) were the main components of the diet of *A. cristatellus*, while soft prey (caterpillars, moths, butterflies and flies) made up only 24% of the diet. Similarly, Andrews (1979) showed that the stomach contents of *A. oculatus* from a cacao plantation near Calibishie (and thus a habitat comparable to our studied sites) contained primarily Formicidae (ants; 41%) and Diptera (soft prey; 3%) in their stomach contents. Moreover, despite seasonal and habitat variation in the diet of *A. oculatus*, ants are abundant across the habitats of Dominica and remain the main prey consumed by this species (Bullock *et al.*, 1993). Thus, the similarity in diet between the species in their respective



**Figure 2.** Least-square means from the linear mixed-effect models testing the first PCA axis (mean  $\pm$  SE) – representing head morphology and SVL – across species (green: *Anolis cristatellus*, orange: *Anolis oculatus*) and contexts (allopatry and sympatry) for males (A) and females (B) from Calibishie.

native ranges and the abundance of their main food resource (ants) across the island of Dominica makes it less likely that diet was a driver of the species differences observed between *A. oculatus* and *A. cristatellus*.

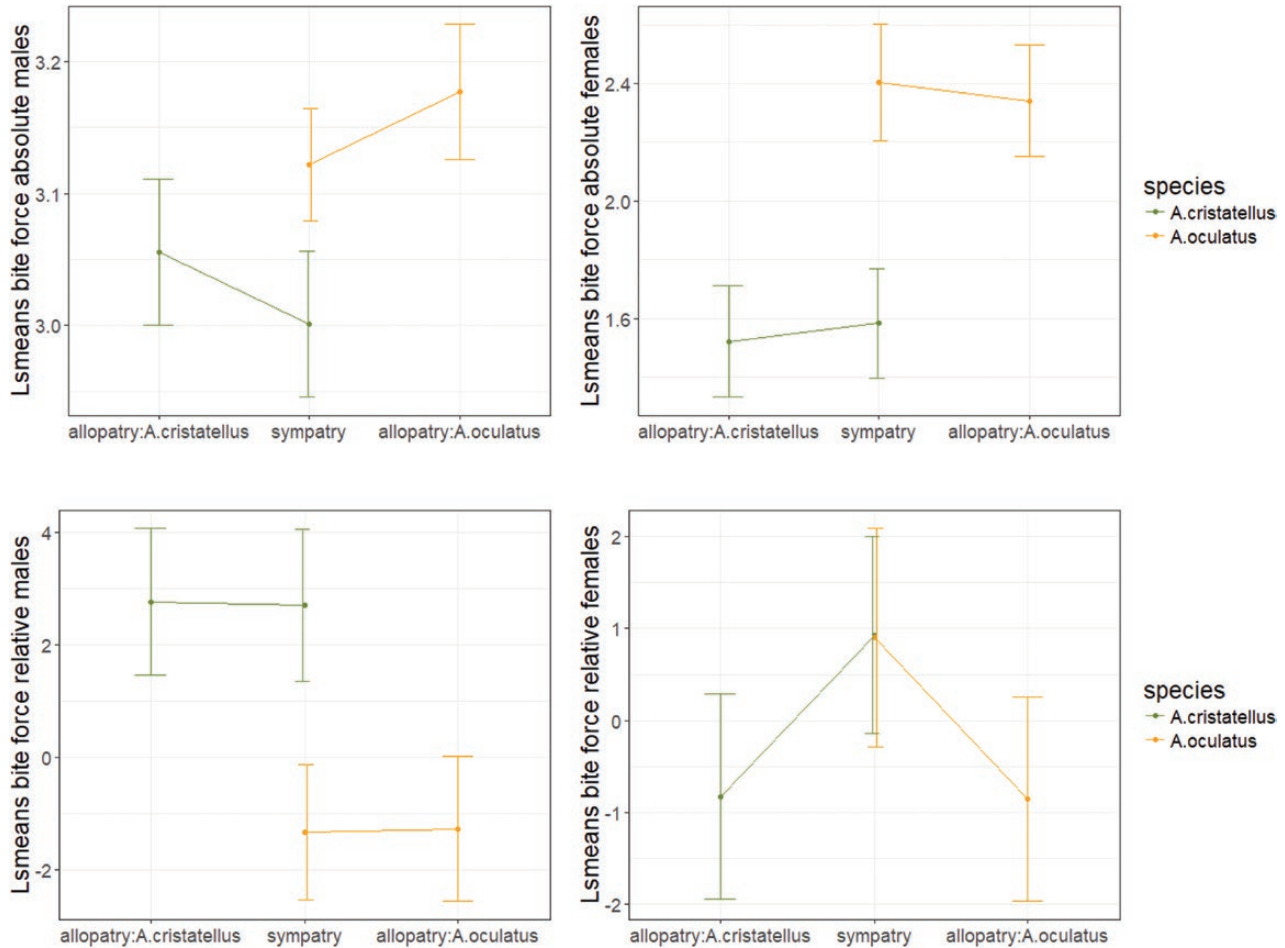
Alternatively, the higher bite force of *A. oculatus* may be linked to greater intraspecific competition (Lailvaux *et al.*, 2004; Husak *et al.*, 2006; Lailvaux & Irschick, 2007), sexual selection (Lappin & Husak, 2005; Herrel *et al.*, 2009) or predation pressure (Leal & Rodriguez-Robles, 1995). For instance, Donihue *et al.* (2016) demonstrated that direct intraspecific agonistic encounters, and not diet, played a role in the evolution of greater bite force in *Podarcis erhardii*. Further comparative study on intraspecific competition in Puerto Rico and Dominica is needed to infer its potential effect on the species differences in bite force and head morphology. Nonetheless, the evolutionary history of the two species may allow us to make predictions: *A. oculatus* being the sole native species on Dominica may experience higher intraspecific competition compared to *A. cristatellus* which occurs with nine other anole species in Puerto Rico (Losos, 2009).

Finally, greater absolute bite force goes hand in hand with a larger body and head size (Herrel *et al.*, 2001a; Lailvaux *et al.*, 2004; Husak *et al.*, 2006; Henningsen & Irschick, 2012; Bush *et al.*, 2016) and this study confirmed the strong positive correlation between size and absolute bite force. While species differences in head and body size seem to suffice to explain differences in absolute bite force between species for females, relative to their size, *A. cristatellus* males bite harder than *A. oculatus* males. This result suggests the presence

of additional drivers of male bite force such as species differences in head shape (Herrel *et al.*, 2001a, 2004b, 2007; Anderson *et al.*, 2008) and muscle architecture (Herrel *et al.*, 1999, 2006; Wittorski *et al.*, 2015).

#### *The effect of interspecific competition on fighting ability and diet?*

A critical assumption of our study is that head morphology and bite force play a role in determining the outcome of interspecific interactions. Research on this topic in anoles and other lizards remains ambiguous and needs further work. For instance, in interspecific encounters among skinks (*Egernia* sp., *Eulamprus* sp.; Langkilde & Shine, 2007) and among anoles (*Anolis sagrei* and *A. carolinensis* females; Edwards & Lailvaux, 2013), dominance was not related to the relative body size or bite force of the individuals; rather, members of some species regularly dominated others regardless of phenotype. Nonetheless, the role of head morphology and bite force in fighting ability has been demonstrated in animals in general (Adams, 2004; Herrel *et al.*, 2005; Huyghe *et al.*, 2005; Husak *et al.*, 2006; Santana *et al.*, 2010) and in anoles in particular (Lailvaux *et al.*, 2004; Lailvaux & Irschick, 2007), and previous studies have argued in favour of the role of bite force during interspecific fighting (Downes & Bauwens, 2002; Adams, 2004; Herrel *et al.*, 2004b). Indeed, *Podarcis sicula* has been shown to dominate the closely related species *Podarcis melisellensis* during direct agonistic encounters (Downes & Bauwens, 2002) and to have greater bite force (Herrel *et al.*,



**Figure 3.** Least-square means from the linear mixed-effect models testing the absolute (log-transformed, top panels) and the relative (the residuals of the linear regression between bite force and SVL, bottom panels) bite forces (mean  $\pm$  SE) across species (green: *Anolis cristatellus*, orange: *Anolis oculatus*) and contexts (allopatry and sympatry) for males (left panels) and females (right panels) from Calibishie.

2004b). Along the same lines, aggressive interference with biting has probably driven divergence in head morphology in the salamanders *Plethodon teyahalee* and *Plethodon jordani* (Adams, 2004).

Alternatively, resource-use competition may also induce shifts in bite force: head divergence is the result of exploitative competition for food and is linked to biomechanical differences in jaw closure in *Plethodon cinereus* and *Plethodon hoffmani* (Adams & Rohlf, 2000). Finally, Losin (2012) and Grether *et al.* (2013) showed that sympatric *A. cristatellus* males from Florida – where they compete for resources and fight with *A. sagrei* – possessed shorter, broader and deeper heads as well as a greater bite force than their allopatric counterparts from Puerto Rico. The underlying process of these shifts remains unknown, however.

In Dominica, *A. cristatellus* and *A. oculatus* compete for resources (ecological displacement in perch height; Dufour *et al.*, 2017) and interfere directly through

agonistic encounters (Fig. 1; C. M. S. Dufour *et al.*, unpubl. data). Unexpectedly, the present study did not reveal significant effects of interspecific competition on the traits measured. Yet, exploitative competition for food may not take place because the main food resource of both species (ants; Wolcott, 1924; Andrews, 1979) appears to be abundant in Dominica (Bullock *et al.*, 1993).

Nevertheless, the role of the recent interspecific competition and particularly interference competition between *A. cristatellus* and *A. oculatus* deserves more attention. Indeed, the Calibishie populations, which have only been in sympatry for 2 years, may have not had enough time to evolve differences in bite force in response to the new interspecific competition. A previous study revealed that rapid microhabitat-use displacement was accompanied by adaptive morphological changes (limb and toepad morphology) only in areas where *A. cristatellus* arrived more than

a decade ago (Dufour *et al.*, 2017). Consequently, the habitat-use behavioral change was suggested to be one of the first responses to the recent interspecific competition observed in Calibishie (Dufour *et al.*, 2017). Similarly, it is possible that interspecific competition between the invasive and native species has driven the evolution of agonistic behaviours – which are more likely to evolve first (Duckworth, 2009; Anderson & Grether, 2010) – and may only subsequently lead to changes in head morphology and bite force. In addition, physiological changes in sympatry may occur first and may secondarily drive shifts in bite force and head morphology. Compared to other Puerto Rican *Anolis*, *A. cristatellus* has both higher circulating testosterone levels and greater bite force (Husak & Lovern, 2014).

#### *What are the potential drivers of the invasion success of A. cristatellus in Calibishie?*

Although dominance status is an important component of invasion success in numerous species (Duyck *et al.*, 2004; Engel & Tollrian, 2012), it appears that *A. oculatus*, with stronger biting capabilities, would have the advantage during interspecific fights. This makes the fighting ability hypothesis unlikely as a main determinant of the successful establishment of *A. cristatellus* at the first stages of the invasion process in Dominica. Moreover, the literature suggests that ants (the main food resource for both species; Wolcott, 1924; Andrews, 1979) are abundant and that the relative distribution of hard vs. soft prey is homogeneous along the perch height (Bullock *et al.*, 1993), making it improbable that the dominant food exploitation hypothesis can explain the invasion success of *A. cristatellus*. Therefore, other processes are probably responsible for the rapid invasion of *A. cristatellus* in Calibishie. For instance, *A. cristatellus* may act as a vector to a parasite that can potentially strongly affect the native *A. oculatus* (Schall, 1992; along these lines, it is of note that we observed parasites in *A. cristatellus* from Calibishie and Losin (2012) observed them in populations from Puerto Rico). Alternatively, greater risk-taking behaviour in open areas (Lapiedra *et al.*, 2017), faster reproduction (Holway & Suarez, 1999; Duyck *et al.*, 2004; Iles *et al.*, 2016), a better immune system (Prenter *et al.*, 2004) or a more efficient metabolism (Schroder *et al.*, 2009; Strubbe & Matthysen, 2009; Engel & Tollrian, 2012) are among the potential factors that may enhance the establishment and spread of *A. cristatellus* across the island of Dominica. These factors remain to be tested.

To conclude, head morphology and bite force are correlated in both species and appear unlikely to determine the establishment success of *A. cristatellus* in Dominica under interspecific interference as the native

species – *A. oculatus* – has a greater absolute bite force than the invasive species. Moreover, a review of the literature reveals that competition for food between the two species seems unlikely and thus might not drive the successful invasion of *A. cristatellus* in Dominica. Consequently, future work is needed to test the role of establishment-advantageous behaviour, life history traits, metabolism and parasite resistance as alternative hypotheses to explain the invasiveness of *A. cristatellus* in Dominica.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

**Table S1.** Raw data of the body mass, SVL, head morphological traits and bite force (absolute, in Newtons) of *Anolis oculatus* and *A. cristatellus* males (m) and females (f) in allopatry and sympatry according to the site (i.e. population) of sampling (Calibishie, Dominica, 2016).

**Table S2.** Eigenvalues and relative factor loadings (SVL and head traits) on the first two PC axes for males and females.