The effect of recent competition between the native *Anolis oculatus* and the invasive *A. cristatellus* on display behavior

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Invasive species are a global threat to biodiversity. Cases where the invasion has been tracked since its beginning are rare, however, such that the first interactions between invasive and native species remain poorly understood. Communication behavior is an integral part of species identity and is subject to selection. Consequently, resource-use and direct interference competition between native and invasive species may drive its evolution. Here, we tested the role of interactions between the recently-introduced invasive lizard *Anolis cristatellus* and the native *Anolis oculatus* on variation in behavior and communication in Calibishie (Dominica). From May-June 2016, we filmed 122 adult males of both species displaying in banana farms under two contexts (allopatry and sympatry). We then recorded i) the proportion of time spent displaying and ii) the relative frequency of dewlap versus push-up displays. To control for habitat variation, we measured and compared the habitat characteristics (canopy cover and habitat openness) of 228 males in allopatry and sympatry. While the habitat characteristics and total display time did not differ between the contexts for the two species, the proportion of display-time spent dewlapping by *A. cristatellus* decreased in sympatry. The display of *A. oculatus* did not differ between the contexts, however. Shifts in microhabitat use, predation pressure, or interspecific interference are potential factors which might explain the behavioral changes in display observed in *A. cristatellus*. This study highlights the role of behavioral traits as a first response of an invasive species to recent competition with a closely-related native species.

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2   *cristatellus* on display behavior

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11   **ABSTRACT**

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13   since its beginning are rare, however, such that the first interactions between invasive and native

14   species remain poorly understood. Communication behavior is an integral part of species identity

15   and is subject to selection. Consequently, resource-use and direct interference competition between

16   native and invasive species may drive its evolution. Here, we tested the role of interactions between

17   the recently-introduced invasive lizard *Anolis cristatellus* and the native *Anolis oculatus* on

18   variation in behavior and communication in Calibishie (Dominica). From May-June 2016, we

19   filmed 122 adult males of both species displaying in banana farms under two contexts (allopatry

20   and sympatry). We then recorded i) the proportion of time spent displaying and ii) the relative

21   frequency of dewlap versus push-up displays. To control for habitat variation, we measured and

22   compared the habitat characteristics (canopy cover and habitat openness) of 228 males in allopatry

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24   contexts for the two species, the proportion of display-time spent dewlapping by *A. cristatellus*

25   decreased in sympatry. The display of *A. oculatus* did not differ between the contexts, however.

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27   which might explain the behavioral changes in display observed in *A. cristatellus*. This study

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29   competition with a closely-related native species.

INTRODUCTION

30

31   Invasive species are a global threat to biodiversity, driving species to extinction and

32 imperiling ecosystems (Parmesan, 2006; Van der Putten, 2012). Therefore, understanding how

33 invasive species successfully establish in new environments and their impacts on native species

34 have become some of the main contemporary challenges. However, only rarely are invasions

35 tracked from their beginning. Yet, the first years of native-invasive species competition often

36 determine its outcome (Puth & Post, 2005). By consequence, recent species invasions constitute

37 an important field of research in evolutionary conservation biology by providing a natural

38 experimental setting to test the role of interspecific competition on species evolution in action.

39   Evolutionary biologists have often considered behavior as an inhibitor of evolutionary

40 change (Bogert, 1949), allowing individuals to avoid selection imposed by novel ecological

41 contexts (reviewed in Huey, Hertz, & Sinervo, 2003; Duckworth, 2008; Muñoz & Losos, 2017).

42 However, behavioral changes may directly alter selective pressures (Mayr, 1963; Duckworth,

43 2008), insofar as they modify the interaction between individuals and their environment by

44 determining how organisms forage (Grant & Grant, 2014), avoid predators (Losos, Schoener &

45 Spiller, 2004), mate (Lande, 1981), maintain homeostasis (Muñoz & Losos, 2017), and respond to

46 competitors (Anderson & Grether, 2010). From this perspective, while ecologists have focused on

47 genetic, ecological and life-history characteristic of invasive species, the behavioral mechanisms

48 determining the outcome of native-invasive species competition deserve more attention (Holway

49 & Suarez, 1999; Mooney & Cleland, 2001). For example, native Californian ants were displaced

50 by the invasive Argentine ant (*Lepithema humile*) due to behavioral adaptations of the invasive

51 species (Holway, 1999; Holway & Suarez, 1999; Human & Gordon, 1999).

52 Communication is subject to natural and sexual selection and is at the forefront of species

53 divergence and recognition processes (Ord, Stamps & Losos, 2010; Macedonia et al., 2013; Wong

54 & Candolin, 2015). Exploitative (resource use; Huber & Podos, 2006; Huber *et al.*, 2007), direct

55 interference (Anderson & Grether, 2010), and reproductive (Höbel & Gerhardt, 2003) competition

56 between closely related species may drive its evolution. As a result, communication and display

57 behavior are particularly likely to evolve in the context of interactions between native and invasive

58 species. Nonetheless, despite the potential of invasive species to exert selection on native signalers

59 (Servedio, 2004), the role of native-invasive species competition in the evolution of

60 communication behavior remains poorly studied (Candolin & Wong, 2012).

61 The present study aims to examine changes in communication and display behavior during

62 the first stages of an invasion. Specifically, we studied interspecific interactions between an

63 invasive species, *Anolis cristatellus*, from Puerto Rico and the native *Anolis oculatus* on the island

64 of Dominica. The introduction history of *A. cristatellus* has been well documented in Dominica as

65 this species was inadvertently introduced in 1998-2000 on the south Caribbean coast (Eales, Thorpe

66 & Malhotra, 2008, 2010). Since then, *A. cristatellus* arrived in Calibishie in the North-eastern

67 region no earlier than 2014. The species have been shown to fight with each other and diverge in

68 their microhabitat use (i.e. perch height) in sympatry (Dufour, Herrel & Losos, 2017). In addition,

69 because the spread of *A. cristatellus* has been patchy (due to the random spread of this species

70 along the main road), allopatric populations occur in Calibishie, allowing the comparison of

71 behavioral and ecological traits in the two contexts (i.e. allopatry vs. sympatry) for the two species.

72 Lizards of the genus *Anolis* have a colorful and retractable throat fan (dewlap) used to

73 attract females, and repel rivals and predators (Jenssen, 1977; reviewed in Losos, 2009). Display

74 behavior (mostly observed in males) is composed of a specific sequence of dewlap extensions and

75   push-ups (Fig.1). Both push-up display and dewlap extensions may be used as long distant signals

76   (Losos, 1985; Fleishman, 1992; Irschick & Losos, 1996; Ord & Stamps, 2008) but their relative

77   functions are not well-known. Nonetheless, while the vertical body movements appear to be

78   equally important for fights in all anoles (Lailvaux & Irschick, 2007), the dewlap extension display

79   seems to be more frequent in more territorial species (Hicks & Trivers, 1983; Losos, 1990; Irschick

80   & Losos, 1996).

81   Microhabitat motion (Ord et al., 2007; Ord & Stamps, 2008), predation (Leal & Rodriguez-

82   Robles, 1997), and species recognition (Ord & Martins, 2006; Macedonia et al., 2015) are all

83   important drivers that shape anole display behavior and which might be impacted by interspecific

84   competition. For instance, the commonly observed perch use divergence resulting from

85   interspecific competition in *Anolis* lizards (Williams, 1972, 1983; Stuart et al., 2014; Dufour,

86   Herrel & Losos, 2017) might induce new microhabitat pressures in terms of predation, light or

87   motion background environment. In addition, interspecific interference (Grether et al., 2013) and

88   reproductive competition (Ord & Martins, 2006) might shape the display in anoles (but see Hess

89   & Losos, 1989).

90   From May-June 2016, we filmed male *A. oculatus* and *A. cristatellus* displaying in the field

91   and recorded i) the proportion of time spent displaying and ii) the relative frequency of dewlap

92   versus push-up displays. To test the effect of interspecific competition on the measured traits, we

93   took advantage of the fact that allopatric and sympatric populations of the two species live in

94   similar environments (banana farms) within the same climatic and altitudinal region. We also

95   tested whether the general habitat characteristics (i.e. canopy cover and habitat openness) were

96   similar in allopatry and sympatry. If display behavior is one of the first responses to recent

97   interspecific competition, its duration, characteristics, or both should differ in sympatry compared to

98   allopatry, assuming that habitats are similar. Alternatively, differences in habitat characteristics

99   between allopatric versus sympatric populations may lead to differences in display behavior

100 independently of effects of interspecific competition.

101 **MATERIAL AND METHODS**

102 This study was performed under the research permit from the Ministry of Agriculture and

103 Fisheries, Forestry, Wildlife and Parks division of Dominica and with all the IACUC (n° 26-11)

104 authorizations from Harvard University.

105 **Study sites and species**

106 From May 1st – June 9th 2016, we sampled four sites at which both species occurred ("sympatric"),

107 two sites at which only *A. cristatellus* occurred and three sites at which only *A. oculatus* occurred

108 (the latter two sites termed "allopatric") within the Calibishie region in Dominica (Fig.2). The

109 allopatric populations of the invasive species may be the result of the extinction of the native

110 species. Nonetheless, the recent arrival of *A. cristatellus* in Calibishie –2014—and the fact that we

111 recorded extremely low population densities of *A. oculatus* (and no *A. cristatellus*) in some banana

112 farms suggest that the allopatric populations of the invasive species result from its establishment

113 in naturally unoccupied banana farms. To minimize the influence of the habitat characteristics on

114 display behavior, populations were sampled in banana farms. Each site was sampled on three to

115 five consecutive days. To prevent the risk of re-sampling the same individual within a field session,

116 lizards were captured by noose or hand and marked with a non-toxic marker after recording and

117 filming. Each sampled individual was replaced at the exact same spot within 10 hours after capture.

118 **Display behavior**

119   A total of 122 adult males, observed for the first time in a sitting position (*A. cristatellus* in

120   allopatry (n=23) and sympatry (n=30); *A. oculatus* in allopatry (n=31) and sympatry (n=38)) were

121   video recorded directly in the field. To record undisturbed behavior, the camera was positioned

122   perpendicular to the long axis of the focal lizard in the horizontal plane and at a distance of at least

123   five meters. Recording started when the focal individual initiated the first display. Recording

124   sessions (mean ± SD: 8.24 ± 3.20 minutes) were long enough to observe several displays while

125   maximizing the number of tested individuals (the recording stopped when the lizard moved away).

126   With the software JWatcher, i) the proportion of time spent displaying and ii) the proportion of

127   display-time spent dewlapping versus push-ups were recorded by the same observer (all displays

128   were categorized as either dewlap or push-up displays; our metric was the proportion of display

129   time spent in dewlap displays, which is a measure of the relative time spent in the two types of

130   displays).

131   **Habitat characteristics**

132   The habitat characteristics of a total of 81 *A. cristatellus* and 147 *A. oculatus* adult males were

133   determined in allopatry and sympatry by measuring the canopy cover (as the number of squares

134   with more than 50% of visible sky, measured with a densitometer) and the habitat openness

135   (distance in cm to the closest perch available at the same horizontal plan than where the focal lizard

136   was spotted) from the perch where the lizard was initially observed.

137   **Statistical analyses**

138   Statistical analysis was conducted with R-v3. (R Development Core team, 2011). Normality and

139   heteroscedasticity of distributions were verified graphically (data were log-transformed when

140   necessary). The proportions of i) total displaying and ii) relative frequency of dewlap versus push-

141   up displays were analyzed with linear mixed effect models, testing for the effect of context

142 (allopatry versus sympatry), species and the interaction between the two as factors and site as

143 random effect. Linear mixed effect models were performed on the log-transformed canopy cover

144 and habitat openness data, with context as factor and site as random effect. When a two-way

145 interaction was significant, post hoc analyses (Tukey test) were performed by separating the two

146 species and testing the effect of context.

147 **RESULTS**

148 **Display behavior**

149 The proportion of time spent displaying did not differ significantly between the two contexts (Tab. 1,

150 Fig. 3).

151 The proportion of display-time spent dewlapping versus performing push-up displays was

152 significantly lower in sympatry compared to allopatry for *A. cristatellus* (Tukey, d.f. = 7, t = 3.121,

153 P = 0.016), but did not change for *A. oculatus* (Tukey, d.f. = 7, t = 0.323, P = 0.756, Fig. 4, Tab.1).

154 **Habitat characteristics**

155 Canopy cover (Fig. 5) and habitat openness (Fig. 6) did not differ significantly in allopatry and

156 sympatry for the two species (Tab. 1)

157 **DISCUSSION**

158 Invasive species are a global scourge, but data on the interactions between native and invasive

159 species when they first come into contact are rare (Puth & Post, 2005). Our study revealed that,

160 only two years after their arrival in Calibishie, males of *A. cristatellus* showed a shift in the type

161 of displays performed in sympatry compared to allopatry, performing relatively more push-ups

162 and fewer dewlap displays. No change was observed for the native *A. oculatus*. The similarity of

163   the habitat characteristics (i.e., canopy cover and habitat openness) between the two contexts

164   suggests an important role for recent competition in driving the behavioral change observed in the

165   invasive species. The following discussion addresses the potential role of predation, microhabitat

166   use, and agonistic interaction as possible explanations for the differences between species in their

167   response to sympatry.

168   Microhabitat use has been shown to be an important driver shaping communication

169   behavior in species in general, and in *Anolis* lizards in particular (Ord, Stamps & Losos, 2010).

170   For instance, the visual motion background and predation pressure are among the main factors

171   driving communication behavior in anoles and in *A. cristatellus* in particular (Leal & Rodriguez-

172   Robles, 1995, 1997; Ord et al., 2007). Moreover, the role of interspecific competition in

173   microhabitat species divergence has been demonstrated in anoles (Schoener, 1970; Williams,

174   1972, 1983; Losos, 2009; Stuart et al., 2014). Nonetheless, studies on the direct link between recent

175   habitat character displacement and the evolution of communication behavior are lacking and no

176   such studies have been published on anoles.

177   In Dominica, and in Calibishie in particular, *A. cristatellus* and *A. oculatus* diverged in

178   sympatry in perch height: the invasive species moved downward toward the ground while the

179   native species used higher perches compared to populations in allopatry (Dufour, Herrel & Losos,

180   2017). This microhabitat divergence might be correlated with a different visual background,

181   potentially driving display variation. Indeed, the visual background is expected to be more variable

182   higher up (due to foliage motion) than on the ground. It has been shown that the duration and the

183   speed of the display of *Anolis* lizards increased under a visually motion background habitat (Ord

184   et al., 2007; Ord, Stamps & Losos, 2010). Moreover, the Australian lizard *Amphibolurus muricatus*

185   changed the structure of his communication behavior and increased the duration of its tail display

186   in a habitat characterized by background movement (Peters, Hemmi & Zeil, 2007). In our study, a

187   more stable background lower to the ground may be associated with the shift toward displaying

188   more with push-ups and less with dewlap displays observed in *A. cristatellus* in sympatry. Indeed,

189   the time and energetic costs of the dewlap extension display may induce a trade-off between

190   conspicuousness and metabolic cost (Vehrencamp, Bradbury & Gibson, 1989; Marler et al., 1995;

191   Clark, 2012). Why the inverse pattern is not observed in *A. oculatus*, which perches higher in

192   sympatry, is unclear, but could be related to a less drastic difference of the visual-motion

193   background between the two contexts for this species as it is always perching relatively high in

194   trees.

195   The ecological character displacement in microhabitat use may also induce differences in

196   predation pressure between the two contexts. Indeed, terrestrial anole predators such as rats or

197   *Ameiva* lizards were found in abundance at the study sites. *Anolis cristatellus* performs a push-up

198   display in presence of a snake predator and increases the rate thereof when the predator is closer

199   (Leal & Rodriguez-Robles, 1997). Moreover, the dewlap is a colorful visual signal (Losos, 1985;

200   Leal & Fleishman, 2004; Nicholson, Harmon & Losos, 2007; Ng et al., 2013; Ingram et al., 2016)

201   and conspicuousness has been shown to increase predation rate in lizards (Fitch & Henderson,

202   1987; Stuart-Fox et al., 2003; Husak et al., 2006). By consequence, the increase of the push-up

203   display proportion of *A. cristatellus* in sympatry perching lower to the ground may be the result of

204   evolutionary trade-off between predation and communication (Steinberg et al., 2014).

205   Alternatively, direct agonistic encounters between the two species might drive the display

206   behavior shift observed in *A. cristatellus* in sympatry. Indeed, we observed the native *A. oculatus*

207   initiating interspecific agonistic encounters, forcing *A. cristatellus* to move downward. Moreover,

208   *A. oculatus* has a bigger head and can bite harder than *A. cristatellus*, suggesting the dominant

209   status of the native species during interspecific fights (Dufour, Losos & Herrel, in revision). Thus,

210   by decreasing dewlap extension time, *A. cristatellus* might be more cryptic in sympatry to avoid

211   the agonistic encounters with *A. oculatus.*

212   It is possible that the two types of display observed in *A. cristatellus* might be the result of

213   different social contexts (assertion, courtship or challenge; Carpenter., 1967; Jenssen, 1977)

214   encountered in allopatry and sympatry. However, more recent studies have revealed that the

215   characterization of different display types depending to the social context confuse the form and

216   the function of the displays (Decourcy & Jenssen, 1994; Lovern et al., 1999; Bloch & Irschick,

217   2006).

218   **CONCLUSION**

219   To conclude, this study reveals the presence of character displacement (Brown & Wilson, 1956)

220   in elements of the behavioral display in the invasive species *A. cristatellus* in Dominica. More

221   research is required to elucidate whether these display shifts are plastic or the result of genetic

222   change. As plasticity has been suggested to account for most of the display behavior variation in

223   *Anolis* lizards (Ord, Stamps & Losos, 2010), this is also likely the case here. This study represents

224   a rare case in which the impact of competition between native and invasive species is studied at

225   the early stages of the invasion process, highlighting the importance of the communication

226   behavior as one of the first responses to environmental change.

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Figure 1

Anolis cristatellus (A) and *A. oculatus* (B) males displaying (dewlap extension) in Calibishie (Dominica).

Photo source credit: C MS Dufour.

Figure 2

Distribution of the sites sampled (S1-S9) across Calibishie (Dominica). Shading indicates context (allopatry, sympatry) and species sampled.
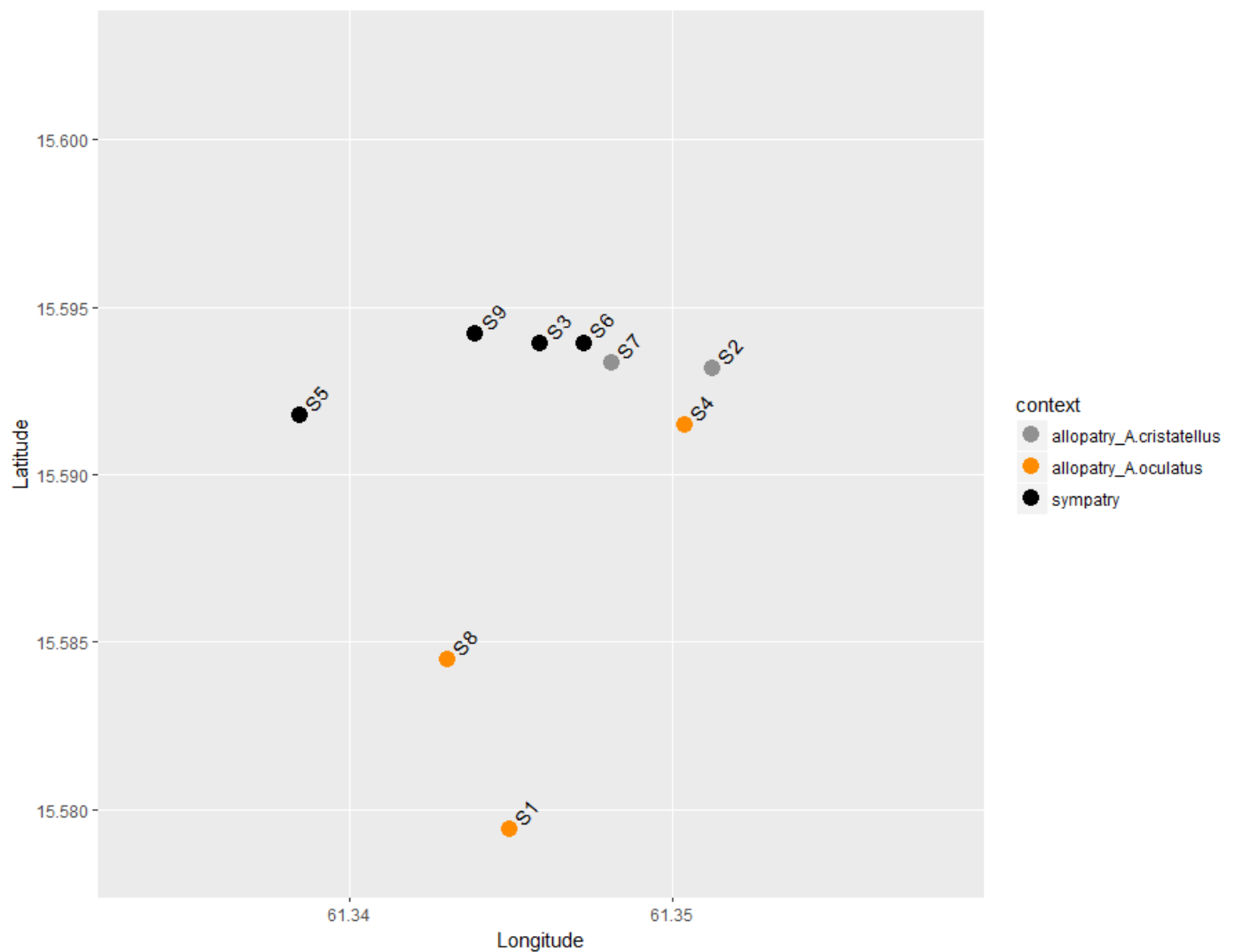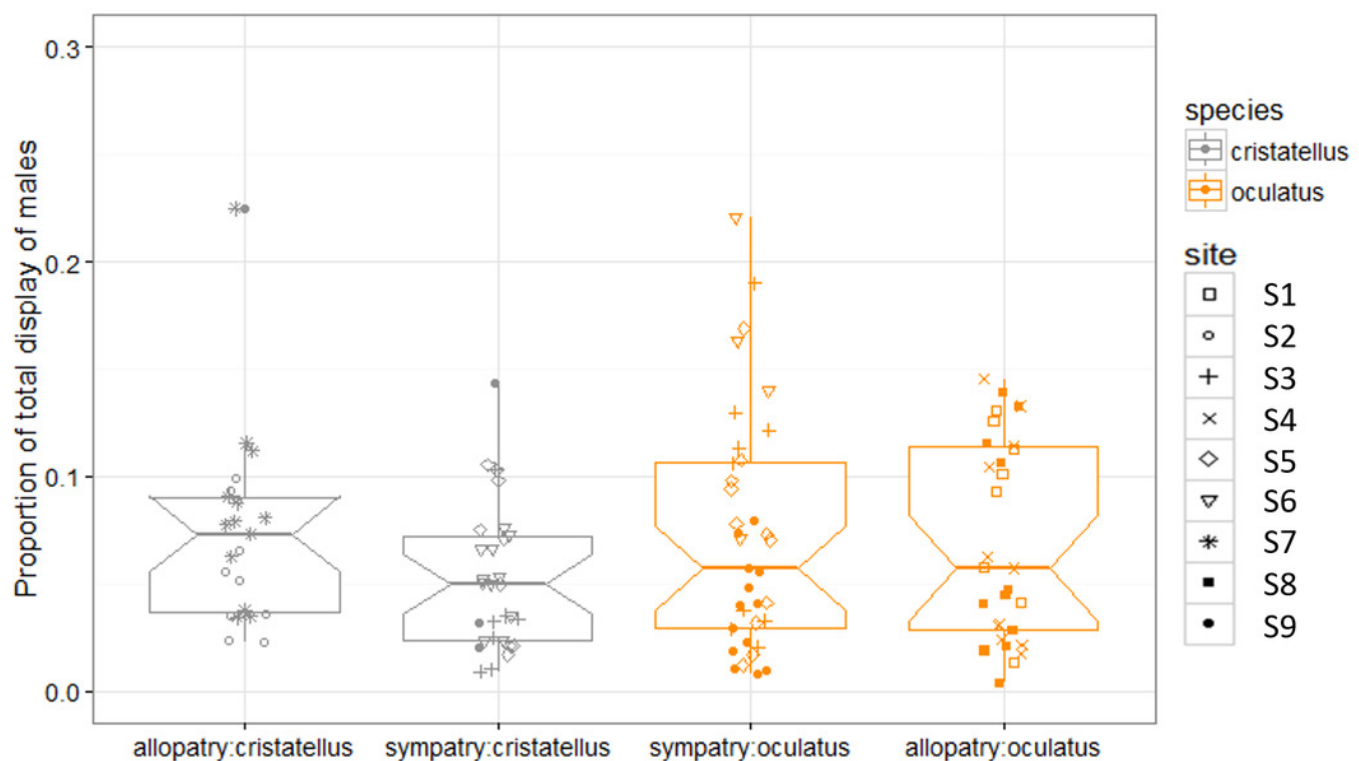
Figure 3

Proportion of time spent displaying for males recorded in Calibishie (2016) across species (grey: *A. cristatellus*, orange: *A. oculautus*) and context (allopatry vs. sympatry) and according to the sites of sampling.

Box-plots (calculated from all individuals) show the median (thick line), first and third quartiles. Non-overlapping notches are roughly equivalent to 95% confidence intervals.
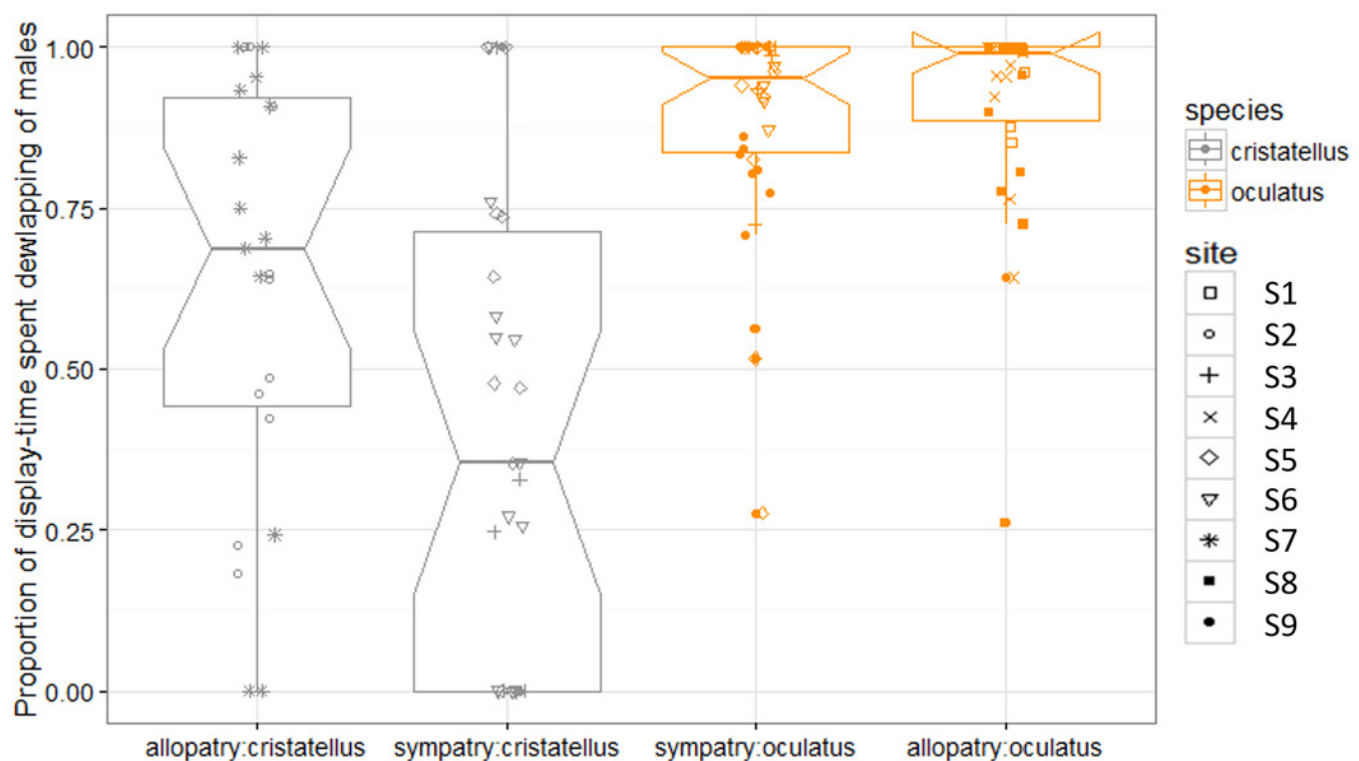
Figure 4

Proportion of display-time spent dewlapping for males video-recorded in Calibishie (2016) across species (green: *A. cristatellus*, orange: *A. oculautus*) and context (allopatry vs sympatry) and according to the sampling sites

Box-plots (calculated from all individuals) show the median (thick line), first and third quartiles. Non-overlapping notches are roughly equivalent to 95% confidence intervals.
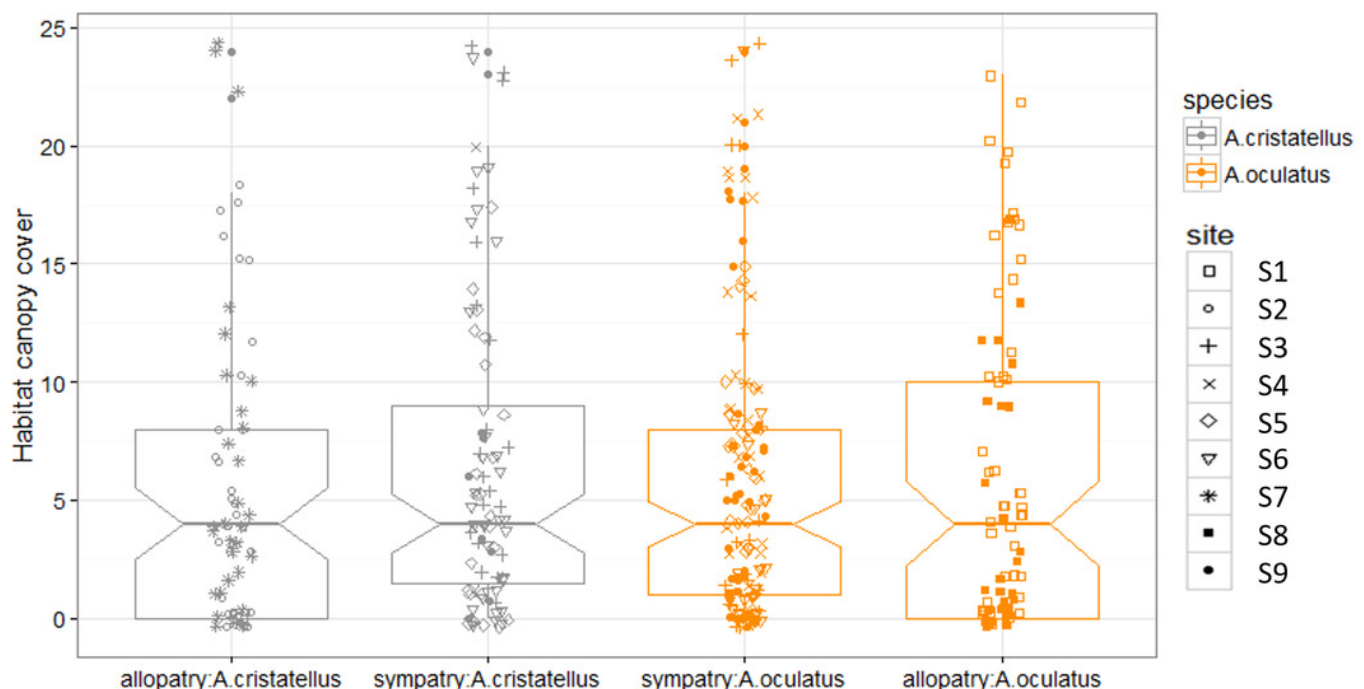
Figure 5

Canopy cover (densiometer) of the habitat used by adult males from Calibishie across the species (grey *Anolis cristatellus*, orange *A. oculatus*) and the context (allopatry, sympatry) and according to the sites of sampling.

Box-plots (calculated from all individuals) show the median (thick line), first and third quartiles. Non-overlapping notches are roughly equivalent to 95% confidence intervals.

Figure 6

Openness (closest perch available) of the habitat used by adult males from Calibishie across the species (grey *Anolis cristatellus*, orange *A. oculatus*) and the context (allopatry, sympatry) and according to the sites of sampling.

Box-plots (calculated from all individuals) show the median (thick line), first and third quartiles. Non-overlapping notches are roughly equivalent to 95% confidence intervals.
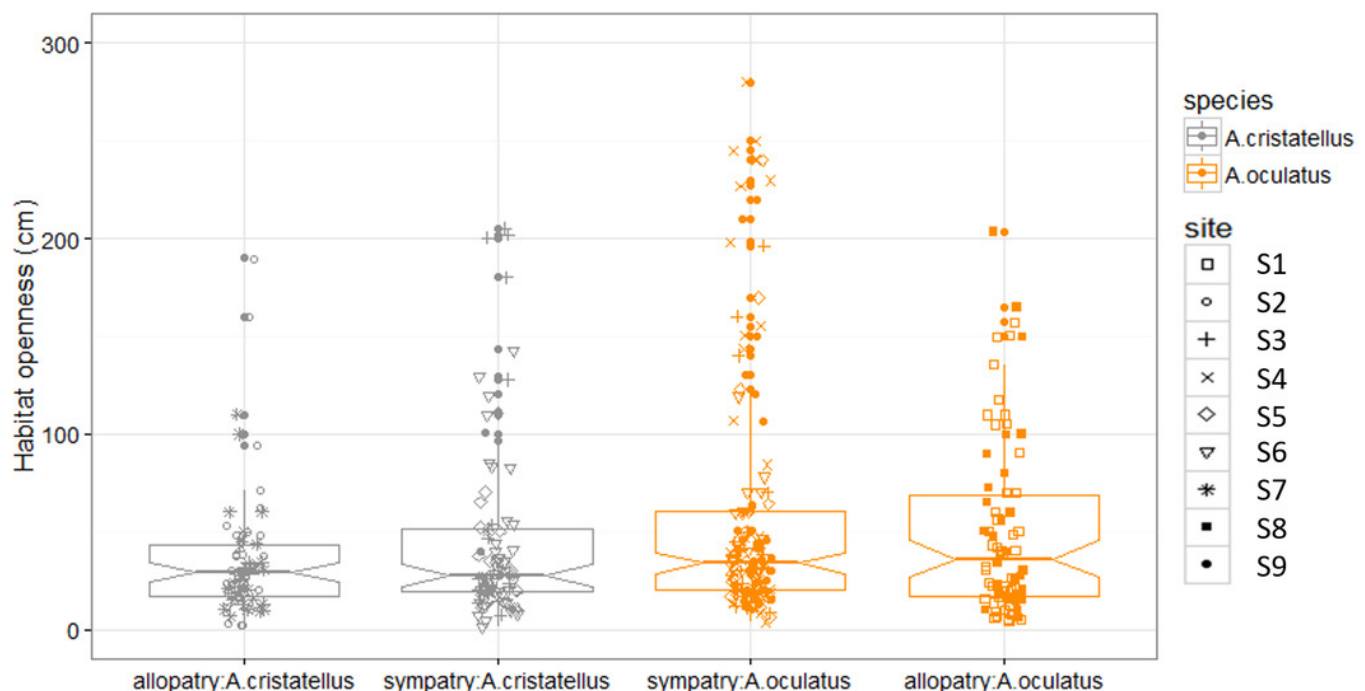
Table 1(on next page)

Statistical results from the final linear mixed-effect models (based on AIC) testing the behavioral and ecological traits of adult males according to the variables (i.e. species, context and the interaction of the two), the site was set as random effect.

1

2   Table 1. Statistical results from the final linear mixed-effect models (based on AIC) testing the behavioral

3   and ecological traits of adult males according to the variables (i.e. species, context and the interaction of

4   the two), the site was set as random effect.

	Trait	Variable	Value	SE	d.f.	*t*-value	*P*-value
BEHAVIOR	Proportion of total display	Intercept	0.062	0.017	112	3.746	<0.001
		Context	-0.011	0.019	7	-0.553	0.597
		Species	0.033	0.016	112	2.064	0.041
	Proportion of display-time spent dewlapping	Intercept	0.636	0.054	111	11.708	<0.001
		Context	-0.225	0.072	7	-3.121	0.017
		Species	0.277	0.072	111	3.869	<0.001
		Context:species	0.205	0.096	111	2.138	0.034
ECOLOGY	Habitat openness	Intercept	3.313	0.095	361	35.052	<0.001
		Context	0.147	0.104	7	1.416	0.199
		Species	0.234	0.097	361	2.418	0.016
	Habitat canopy cover	Intercept	1.469	0.157	361	9.352	<0.001
		Context	0.203	0.189	7	1.076	0.318
		Species	-0.153	0.131	361	-1.163	0.246

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Figure 1. *Anolis cristatellus* (A) and *A. oculatus* (B) males displaying (dewlap extension) in Calibishie (Dominica, 2016). Photo source credit: C MS Dufour.

Figure 2: Distribution of the sites sampled (S1-S9) across Calibishie (Dominica, 2016). Different shapes indicate context (allopatry, sympatry) and species sampled. The grey and white areas represent the sea and land, respectively. The country border (dashed line), the roads (thick grey lines) and the unpaved paths (thin grey lines) are represented. Source of the map: Stamen.

Figure 3. Proportion of time spent displaying by male *Anolis* recorded in Calibishie (Dominica, 2016) across species (*A. cristatellus*, *A. oculatus*) and context (allopatry, sympatry) and according to the sites of sampling. Box-plots (calculated from all individuals) show the median (thick line), first and third quartiles. The lines extending vertically from the boxes indicate the lowest datum still within 1.5 IQR (interquartile range) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile. Individual points beyond these lines represent outliers. The notches indicate 95% confidence intervals so that the distributions differ significantly if the notches do not overlap.

Figure 4. Proportion of display-time spent dewlapping versus performing push-up displays by male *Anolis* video-recorded in Calibishie (Dominica, 2016) across species (*A. cristatellus*, *A. oculatus*) and context (allopatry, sympatry) and according to the sampling sites. Box-plots (calculated from all individuals) show the median (thick line), first and third quartiles. The lines extending vertically from by male *Anolis* the boxes indicate the lowest datum still within 1.5 IQR (interquartile range) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile. Individual points beyond these lines represent the outliers. The notches

indicate 95% confidence intervals so that the distributions differ significantly if the notches do not overlap.

Figure 5. Canopy openness (number of densiometer squares out of 24 with more than 50% of visible sky) of the habitat used by adult male *Anolis* from Calibishie (Dominica, 2016) across the species (*A. cristatellus*, *A. oculatus*) and the context (allopatry, sympatry) and according to the sites of sampling. Box-plots (calculated from all individuals) show the median (thick line), first and third quartiles. The lines extending vertically from the boxes indicate the lowest datum still within 1.5 IQR (interquartile range) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile. Individual points beyond these lines represent the outliers. The notches indicate 95% confidence intervals so that the distributions differ significantly if the notches do not overlap.

Figure 6. Habitat openness (distance to closest available perch, cm) of the habitat used by adult male *Anolis* from Calibishie (Dominica, 2016) across the species (*A. cristatellus*, *A. oculatus*) and the context (allopatry, sympatry) and according to the sites of sampling. Box-plots (calculated from all individuals) show the median (thick line), first and third quartiles. The lines extending vertically from the boxes indicate the lowest datum still within 1.5 IQR (interquartile range) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile. Individual points beyond these lines represent the outliers. The notches indicate 95% confidence intervals so that the distributions differ significantly if the notches do not overlap.

66   Table 1. Statistical results from the final linear mixed-effect models (based on AIC) testing the

67   behavioral traits and ecological characteristics of *Anolis cristatellus* and *A. oculatus* adult males

68   according to the variables (i.e. species, context and the interaction of the two). The site was set as a

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	Trait	Variable	Value	SE	d.f.	*t*-value	*P*-value
Behavioral traits	Proportion of total display	Intercept	0.062	0.017	112	3.746	<0.001
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Ecological characteristics	Habitat openness	Intercept	3.313	0.095	361	35.052	<0.001
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	Canopy openness	Intercept	1.469	0.157	361	9.352	<0.001
		Context	0.203	0.189	7	1.076	0.318
		Species	-0.153	0.131	361	-1.163	0.2

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