

Recent biological invasion shapes species recognition and aggressive behaviour in a native species: A behavioural experiment using robots in the field

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Funding information

Fondation Fyssen; Putnam grant

Handling Editor: Sonya Clegg

Abstract

1. Invasive species are a world-wide threat to biodiversity. Yet, our understanding of biological invasions remains incomplete, partly due to the difficulty of tracking and studying behavioural interactions in recently created species interactions.
2. We tested whether the interactions between the recently introduced invasive lizard *Anolis cristatellus* and the native *Anolis oculatus* in Dominica have led to changes in species recognition and aggressive behaviour of the native species.
3. The use of realistic robots allowed us to test the behavioural response of 131 *A. oculatus* males towards relevant and controlled conspecific versus heterospecific stimuli, directly in the field and in two contexts (allopatry vs. sympatry).
4. Our results show that species recognition evolved prior to sympatry in *A. oculatus*. Moreover, interspecific competition resulted in an increase in the time spent displaying and a divergence in the aggressive behaviour of the native species towards conspecifics versus heterospecifics. Inherent species recognition and higher aggressive behaviour may limit species coexistence as they are expected to favour *A. oculatus* during territorial interactions with *A. cristatellus*.
5. While more studies are needed to understand the causes of these behavioural shifts and their consequences on long-term species coexistence, the present study highlights the role of behaviour as a first response to interspecific interactions.

KEYWORDS

Anolis lizards, display behaviour, Dominica, invasive–native species competition, robots, species coexistence

1 | INTRODUCTION

A million species world-wide are threatened with extinction and biological invasions figure among the principal drivers of this biodiversity decline (IPBES, 2019). This threat is further amplified by globalization and global change which blur the natural distribution limits between species. As a consequence, the number of new interactions between native and invasive species has soared. But while the first years of native–invasive species interactions often determine their outcome (Puth & Post, 2005), biological invasions are

rarely tracked from their beginning. Thus, understanding how native species respond to novel biological invasions and how the outcome of these interactions can affect future coexistence or extinction is of general interest.

When two species enter into contact, they may interact directly through agonistic behaviours, which may negatively affect one or both species. These direct interactions are defined as behavioural interference and may place constraints on species coexistence (Duckworth, Belloni, & Anderson, 2015; Pasch, Bolker, & Phelps, 2013, reviewed in Grether, Peiman, Tobias, & Robinson, 2017).

Consequently, a shift in traits that affect behavioural interference (i.e. interspecific encounter rates, species recognition and fighting ability) when species co-occur in sympatry can have direct consequences on species persistence and extinction. For instance, coexistence between two species of damselflies is favoured by better species recognition of territorial male *Hetaerina* which discriminated conspecific and heterospecific intruders based on the differences in wing coloration in sympatry, but not in allopatry (Anderson & Grether, 2010). In addition, expensive aggressive encounters between blue tits and great tits are minimized due to song divergence of the subordinate species—blue tits—in sympatry (Doutrelant, Blondel, Perret, & Lambrechts, 2000; Doutrelant, Hitier, Lambrechts, & Aubin, 1998; Doutrelant & Lambrechts, 2001; Doutrelant, Leita, Giorgi, & Lambrechts, 1999).

Despite the role of behavioural interference in species coexistence, the behavioural component of interspecific interactions has been largely ignored when studying and predicting the impact of biological invasions on native species (but see Holway & Suarez, 1999; Lapiedra, Chejanovski, & Kolbe, 2017; Weis & Sol, 2016). This lack of research may be the result of the following two main obstacles when studying biological invasions in natura: (a) the rare opportunity to track the very early stages of native–invasive species interactions; and (b) the difficulty in studying natural behaviour towards controlled stimulus behaviour in the field. While the first point depends on the timeliness of the study, the second one can be overcome through the use of realistic robots or other technological advances.

The use of robots in ecology is still in its infancy, but is promising in many aspects of the field (Grémillet, Puech, Garçon, Boulinier, & Maho, 2012). In behavioural ecology, the use of realistic robots has allowed tests of animal communication theory (Frohnwieser, Murray, Pike, & Wilkinson, 2016), particularly in lizards (Clark et al., 2015, 2016; Klomp, Stuart-Fox, Cassidy, Ahmad, & Ord, 2017; Macedonia et al., 2015; Macedonia, Clark, Riley, & Kemp, 2013; Ord & Stamps, 2009; Partan, Otovic, Price, & Brown, 2011). Indeed, lizards such as anoles and Galapagos lava lizards present stereotyped visual displays that can be reproduced realistically by robots. Hence, the presentation of robots-producing conspecific versus heterospecific displays in natura revealed that animals show a higher response rate towards conspecifics when the evolutionary history of a species included sympatry (Clark et al., 2015, 2016; Macedonia et al., 2013, 2015; but see Ord & Stamps, 2009). Finally, the use of robots in behavioural experiments in natura releases the constraint of using individuals as a signal while allowing the presentation of relevant and controlled stimuli. Consequently, the advent of 'ethorobotics' (Partan et al., 2011) allows behavioural ecologists to overcome the difficulties in studying interspecific interference in the context of biological invasions.

This study aims to determine whether species recognition and aggressive display of a native species has changed during the first stages of a biological invasion. The Caribbean island of Dominica is naturally occupied by a single species of anole—*Anolis oculatus*—and was invaded by the Puerto Rican lizard *Anolis cristatellus* two decades ago (Eales, Thorpe, & Malhotra, 2010). *Anolis cristatellus* reached the north-eastern region of Dominica not earlier than 2014 (Dufour,

Herrel, & Losos, 2018a). The two species are ecologically and morphologically similar, so much so, that several scientists predicted that the species would compete strongly (Daniells et al., 2008; Malhotra, Thorpe, Hypolite, & James, 2007). Indeed, behavioural interference and indirect competition by resource exploitation between the two species has been documented (Dufour et al., 2018a; Dufour, Herrel, & Losos, 2018b; Dufour, Losos, & Herrel, 2018) and has led to a shift in the display behaviour of the invasive species (i.e. decrease of display-time spent dewlapping; Dufour et al., 2018b) and to ecological character displacement in both species (i.e. on perch height and subsequently limb morphology and toepad traits; Dufour et al., 2018a). In response to recent interspecific competition, behavioural changes appear to precede morphological and physiological changes in both species (Dufour et al., 2018a, 2018b; Dufour et al., 2018). Finally, because the spread of *A. cristatellus* has been patchy, allopatric and sympatric populations can be compared in similar environmental conditions (Dufour et al., 2018a, 2018b). Hence, the situation in Dominica presents a clear test to examine species recognition and aggressive behavioural responses of a native species to a recent invader.

First, we ask whether native populations can distinguish between conspecifics and members of the invasive species with which they have no prior experience. Second, we ask whether the native species responds to the coexistence with the invasive species by shifting the duration and characteristics of its aggressive behaviour. Investigating these questions is facilitated by the use of robots, one of each species, under both controlled (standardized stimuli) and natural (directly in the field) experimental conditions.

2 | MATERIALS AND METHODS

2.1 | Study sites and species

From 14 April to 27 May 2017, we sampled 131 *A. oculatus* males at two sites where only *A. oculatus* occurred (i.e. allopatric sites) and three sites where both *A. oculatus* and *A. cristatellus* occurred (i.e. sympatric sites) within the Calibishie region in Dominica (see, site locations in Supplementary Material 1 and population characteristics in Supplementary Material 2). To minimize the influence of variation in habitat characteristics on display behaviour, populations were sampled in banana farms which are homogeneous in vegetation structure (Dufour et al., 2018b). Each site was sampled on three to six consecutive days.

2.2 | The robots as conspecific and heterospecific signals

We built two robots, one for each species. The body morphology, colour of the dewlap (i.e. extendable throat fan) and display behaviour of the robots were averaged from morphological, spectrometric and display action pattern measurements taken



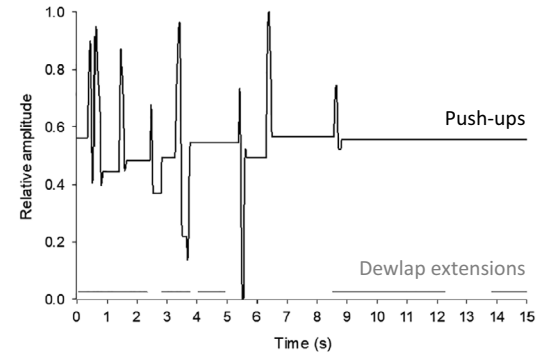
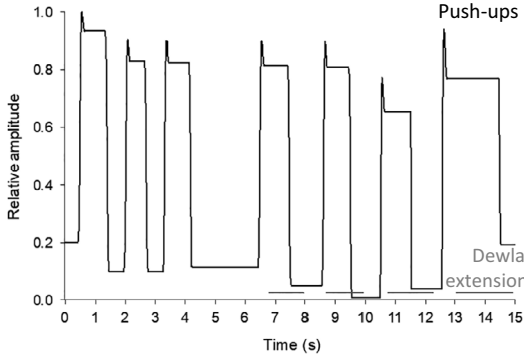
| | <i>Anolis oculatus</i> | | <i>Anolis cristatellus</i> | |
|---------------------------------|--|-------|---|-------|
| | Male | Robot | Male | Robot |
| Photos |  | |  | |
| Size (snout-hip) | 71 mm | | 59 mm | |
| Display action pattern |  <p>Relative amplitude</p> <p>Time (s)</p> <p>Push-ups</p> <p>Dewlap extensions</p> | |  <p>Relative amplitude</p> <p>Time (s)</p> <p>Push-ups</p> <p>Dewlap extensions</p> | |
| Loop: 15s of display, 15s pause | | | | |
| Dewlap ink | Prismacolor Premier ink marker PB-16 orange | | Prismacolor Premier ink marker Center: PB: PB-19 canary yellow Edge: PB-14 pale vermillion | |

FIGURE 1 Morphological and display characteristics of *Anolis oculatus* and *Anolis cristatellus* robots. Photo credits: C.M.S. Dufour

from allopatric individuals (Figure 1; Supplementary Material 3). Complete details of robot construction and display programming methods are provided in Clark et al. (2015) and Macedonia et al. (2013).

2.3 | Response to conspecific and heterospecific robots: An experiment in natura

We performed experiments in the field, from 7 a.m. to 1 p.m. under clear to cloudy skies. First, we carefully scanned the site searching for unmarked adult *A. oculatus* males in a sitting position. We then slowly positioned the robot (randomly assigned as conspecific or heterospecific) at the same height as the focal lizard (on a tripod when the focal lizard's height was >20 cm) and perpendicularly to the long axis of the undisturbed focal lizard (distance from the lizard to the robot $M \pm SE = 112.21 \pm 33.10$ cm) so that the lizard was able to see the robot (Figure 2). When the robot was positioned, the observer slowly walked away and switched on the display program at 2 m from the robot. A video camera was positioned at least 5 m from the lizard at the same height and perpendicular to the focal lizard so that both the robot and the lizard were in the field of view whenever possible



FIGURE 2 *Anolis oculatus* male (background) displaying to a conspecific robot (foreground) in the field (Calibishie, Dominica, 2017). Photo credit: C.M.S. Dufour

(if not, we video-recorded only the focal lizard and said 'start' when the robot started to display). We started recording when the robot was positioned (prior to turning it on) and continued recording until the end of the experiment, 10 min after the robot was turned on or when the lizard moved away, whichever came first (total video duration— $M \pm SE = 9.06 \pm 0.24$ min—did not differ between the two contexts and the two robots, Supplementary Material 4). Recording

duration was long enough to observe several displays while maximizing the number of tested individuals. At the end of the trial, the lizard was captured by noose or by hand and marked with a non-toxic marker to prevent resampling the same individual (each lizard was tested only once). Each sampled individual was replaced at the spot at which it was captured within 10 hr after capture.

2.4 | Description of the display repertoire

We recorded nine behaviours exhibited by *A. oculatus* during displays (Table 1): approach; crest erection; dewlapping only; pati-pato; push-up two legs; push-up two legs and dewlapping; push-up four legs; push-up four legs and dewlapping; tongue out.

2.5 | Recording behaviours with video analysis

The video-based behaviour quantification was performed with the software *JWatcher* (observer: C.M.S. Dufour).

To test whether the robot was perceived as realistic by its visual appearance, its motion or both, we compared the duration of display (divided by total duration of the video) before the robot was turned on, while the robot was turned on and moving, and while it was turned on but inactive ('pauses'). If the robot is realistic, we would expect *A. oculatus* males to display more towards the robot (conspecific and heterospecific) after it has been switched on, during the moving and pause phases (Ord & Stamps, 2009). A subsample of 63 video-recorded *A. oculatus* males was used in this control analysis

(i.e. when the off stage lasted more than 15 s, so that each lizard presented three observations, one for each robot stage).

To compare the response rate of *A. oculatus* males towards conspecific versus heterospecific robots in allopatry ($n = 34$ towards conspecific robots and $n = 37$ towards heterospecific robots) and sympatry ($n = 28$ towards conspecific robots and $n = 32$ towards heterospecific robots), the proportion of time spent displaying D_i (i.e. all of the nine display behaviours combined) was determined per individual as was the duration of time spent displaying divided by the total duration of the experiment (started when the robot was switched on).

$$\text{Proportion of time spent displaying } D_i = \frac{\text{sum of the duration of the nine display behaviours}}{\text{total duration of the video}}.$$

To compare the behavioural composition of the display of the 131 sampled *A. oculatus* males towards conspecific versus heterospecific robots in allopatry and sympatry, the proportion of time spent performing the behaviour B_i was determined so that the following formula was applied for each of the nine display behaviours recorded:

$$\text{Proportion of time spent performing the display behaviour } B_i = \frac{\text{duration of the behaviour } B_i}{\text{total duration of the video}}.$$

2.6 | Statistical analyses

The inherent characteristics of continuous proportional data (i.e. values from 0 to 1 and usually non constant variance across the

| Behaviour | Description | Previously described in <i>Anolis</i> |
|----------------------------------|--|---------------------------------------|
| Approach | The lizard looks and moves towards the robot | Yes |
| Crest erection | The lizard extends its dorsal crest | Yes |
| Dewlapping | The lizard extends its dewlap | Yes |
| Pati-pato | The lizard pushes in and out with its forelimbs, alternating between right and left. The term 'pati-pato' was arbitrarily chosen (the term 'patte' in French means 'leg') | No |
| Push-up two legs | The lizard displays vertical body movements, pushing up on its two forelimbs. The head and chest of the lizard are off the perch during the push | Yes |
| Push-up two legs and dewlapping | The lizard displays vertical body movements, pushing up on its two forelimbs with dewlap extensions simultaneously. The head and chest of the lizard are off the perch during the push | Yes |
| Push-up four legs | The lizard displays vertical body movements, pushing up on its four limbs. Only the feet touch the perch during the push | Yes |
| Push-up four legs and dewlapping | The lizard displays vertical body movements, pushing up on its four limbs with dewlap extensions simultaneously. Only the feet touch the perch during the push | Yes |
| Tongue out | The lizard protrudes its tongue | Yes |

TABLE 1 Description of the display repertoire of *Anolis oculatus* during interaction with the robots. The pati-pato behaviour is described here for the first time in anoles

range of predictors) imply statistical concerns that can be overcome with the use of appropriate analyses such as beta and Dirichlet regression (reviewed in Douma & Weedon, 2019).

2.6.1 | Response to moving robots

To assess whether the lizard's response differed with the state of the robot (off, move or pause), we modelled our response variable D_i —the proportion of time spent displaying—which contained several '0's with biological significance, using a zero-inflated beta regression implemented in R-v3 (R Development Core Team, 2011) in the BRM package (Bürkner, 2018). The zero-inflated beta regression considered a mixture distribution with a binomial distribution (for the zero-inflated part corresponding to the probability that the lizard did not display $p(D_i = 0)$) followed by a beta distribution (conditional on $D_i > 0$; Douma & Weedon, 2019). The model included the robot state as factor, the identity of the lizard as random effect and was run across four chains of 5,000 iterations each (burn-in of 2,500 iterations per chain, one sample per iteration, so a total of 10,000 post-warmup samples) to reach convergence. The phi and zi (zero inflated) estimates were dependent of the robot state.

2.6.2 | Time spent displaying: Response towards conspecific versus heterospecific robots in allopatry and sympatry

Among the 131 lizards, 15 did not display during the test (i.e. proportion of time spent displaying $D_i = 0$) and four displayed continuously (proportion of time spent displaying $D_i = 1$). To avoid the presence of the few '0' and '1' in the dataset, the proportion of time spent displaying D_i was first transformed according to the following equation (Douma & Weedon, 2019):

$$D_i^* = \frac{D_i(n - 1) + 0.5}{n},$$

where D_i^* is the transformation of D_i and n is the total number of observations in the dataset.

To test whether the lizards responded differently towards the two robots and between the two contexts, we modelled our response variable—the scaled proportion of time spent displaying—using beta regression with a logit link function implemented in R in the GLMMTMB package (Brooks et al., 2017). The model tested for the effect of robot, the context and the interaction between the two and included the site as a random effect.

2.6.3 | Behavioural composition of the display

To test whether the lizards displayed different behaviours towards the two robots and between the two contexts, we modelled the

matrix of the proportions of the nine display behaviours using Dirichlet regression implemented in R in the DIRICHLETREG package (Maier, 2015). The model tested for the effect of robot, the context and the interaction between the two. We used the 'alternative' parameterization (i.e. mean proportion of each of the nine behaviours was predicted by the tested factors) and set the non-display behaviour (i.e. basal behaviour) as the base (omitted) component. To our knowledge, mixed effect models for Dirichlet regression have not been implemented in commonly used software so far. To counteract the fact that we were not able to include the site as random effect in the Dirichlet model, we performed a principal components analysis on the nine display behaviours (Supplementary Material 5). The first three axes (that had an eigenvalue > 1) were retained and analysed separately with linear mixed effect models, testing for the effect of robot, the context and the interaction between the two and including the site as a random effect. The results concurred with those from the Dirichlet regression (Supplementary Material 5) so that we decided to present only the results from the most relevant analysis to study continuous proportional data (i.e. Dirichlet regression) in the main manuscript.

3 | RESULTS

3.1 | Response to moving robots

We first tested whether the lizards appeared to be responding to the robots by comparing their proportion of display before and after the robot was activated. The four chains of the zero-inflated beta regression model successfully combined (Supplementary Material 6) and converged (Table 2). Before the robot was turned on, the lizards rarely displayed (only three individuals among the 63 tested), and the probability of a zero was significant (Table 2). But as soon as the robot started to move, lizards began to display (i.e. lower zero-inflation probability, Table 2; Supplementary Material 6). The proportion of time spent displaying by *A. oculatus* differed depending on the activity of the robot (Table 2). *Anolis oculatus* displayed more after the robot was switched on ($M \pm SE$, robot off: $1.81e^{-4} \pm 1.34e^{-4}$, robot move: 0.24 ± 0.02), and there was no significant difference in display behaviour when the robot was moving and when it was paused (robot pause: 0.25 ± 0.03 , Table 2; Supplementary Material 6).

3.2 | Proportion of time spent displaying: Response towards conspecific versus heterospecific robots in allopatry and sympatry

The proportion of time spent displaying by males was significantly higher towards the conspecific robot than those towards the heterospecific robot and independent of whether populations were allopatric or sympatric (Table 3; Figure 3).

TABLE 2 Statistical results of the zero-inflated beta regression on the proportion of display according to the state of the robot (off, move and pause). The estimate, lower and upper 95% credible intervals, the Rhat (Gelman–Rubin statistic, information about the convergence of the model) and the bulk and tail effective samples size of the algorithm is given for the estimate of the mean (logit function), phi (precision, log function) and zi (probability of a zero, logit function) of the model

| Proportion of display | Estimate | Est. error | Lower 95% CI | Upper 95% CI | Rhat | Bulk ESS | Tail ESS |
|---------------------------|----------|------------|--------------|--------------|------|----------|----------|
| Intercept (robot off) | −7.06 | 0.98 | −8.53 | −4.36 | 1.00 | 989 | 1,129 |
| Robot move | 5.00 | 0.94 | 2.37 | 6.35 | 1.00 | 1,445 | 1,145 |
| Robot pause | 5.08 | 0.94 | 2.44 | 6.43 | 1.00 | 1,444 | 1,154 |
| Phi Intercept (robot off) | 5.03 | 1.46 | 1.12 | 7.02 | 1.00 | 1,503 | 1,109 |
| Phi robot move | 1.34 | 1.65 | −1.15 | 5.44 | 1.00 | 1,131 | 1,127 |
| Phi robot pause | 0.94 | 1.57 | −1.30 | 5.08 | 1.01 | 1,083 | 896 |
| Zi Intercept (robot off) | 3.25 | 0.66 | 2.13 | 4.74 | 1.00 | 5,497 | 5,227 |
| Zi robot move | −6.34 | 0.91 | −8.29 | −4.73 | 1.00 | 3,675 | 4,875 |
| Zi robot pause | −7.66 | 1.34 | −10.76 | −5.51 | 1.00 | 3,667 | 3,207 |

TABLE 3 Statistical results of the mixed effects beta regression model on the scaled proportion of display (logit function) according to the context (allopatry, sympatry) and robot ID (conspecific, heterospecific)

| Scaled (proportion of display) in function of factors | Estimate | SE | Z-value | p-value |
|---|----------|-------|---------|---------|
| (Intercept) | −1.396 | 0.203 | −6.874 | <0.001 |
| robot ID (conspecific) | 1.216 | 0.288 | 4.226 | <0.001 |
| context (sympatry) | 0.709 | 0.285 | 2.488 | 0.013 |
| robot ID: context | 0.319 | 0.418 | 0.765 | 0.444 |

In addition, males from sympatric populations displayed more towards the two robots than males from allopatric populations (Table 3; Figure 3).

3.3 | Behavioural composition of the display towards conspecific versus heterospecific robots in allopatry and sympatry

For the crest erection, pati-pato, push-up two legs with and without dewlapping, and tongue out behaviours, there was an effect of the interaction between robot type and context (Table 4): *A. oculatus* males displayed more towards the conspecific robot (compared to the heterospecific robot) in sympatry, but not in allopatry (Figure 4). In addition, *A. oculatus* males displayed more dewlapping, approach behaviour and push-up four legs (with and without dewlapping) towards conspecific robot than heterospecific robot. Finally, *A. oculatus* males dewlapped more in sympatry compared to allopatry (Table 4; Figure 4).

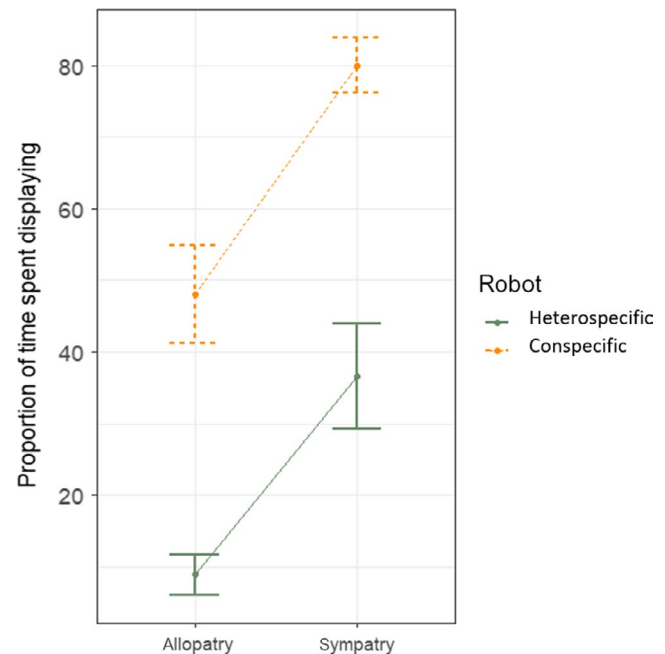


FIGURE 3 Proportion of time spent displaying ($M \pm SE$) by *Anolis oculatus* towards conspecific (orange, dashed line) and heterospecific (green, solid line) robots in allopatry and sympatry

4 | DISCUSSION

Species recognition and shifts in aggressive behaviour are potentially important, yet often neglected, factors that might favour coexistence between native and invasive species at the first stages of a biological invasion. The situation in Dominica allowed us to investigate these possibilities by tracking the behavioural components of the species interaction. The behavioural response of *A. oculatus* to moving robots reveals that the native species discriminates conspecifics from the invasive *A. cristellus* in both allopatry and sympatry. In addition, the native species displayed more and showed a divergence

TABLE 4 Statistical results of the Dirichlet regression model on the proportions of the nine display behaviours (logit function) according to the context (allopatry, sympatry) and robot ID (conspecific, heterospecific)

| Proportion of display | Factors | Estimate | SE | Z-value | p-value |
|----------------------------------|------------------------|----------|-------|---------|---------|
| Crest erection | (Intercept) | -2.789 | 0.177 | -15.782 | <0.001 |
| | context (sympatry) | 0.821 | 0.249 | 3.298 | <0.001 |
| | robot ID (conspecific) | 1.423 | 0.247 | 5.768 | <0.001 |
| | context: robot ID | 1.561 | 0.364 | 4.286 | <0.001 |
| Dewlapping | (Intercept) | -2.529 | 0.175 | -14.447 | <0.001 |
| | context (sympatry) | 0.521 | 0.249 | 2.094 | 0.036 |
| | robot ID (conspecific) | 1.276 | 0.245 | 5.212 | <0.001 |
| | context: robot ID | 0.584 | 0.380 | 1.537 | 0.124 |
| Approach | (Intercept) | -2.777 | 0.177 | -15.719 | <0.001 |
| | context (sympatry) | 0.279 | 0.251 | 1.113 | 0.266 |
| | robot ID (conspecific) | 0.498 | 0.251 | 1.980 | 0.048 |
| | context: robot ID | 0.731 | 0.394 | 1.857 | 0.063 |
| Pati-pato | (Intercept) | -2.962 | 0.178 | -16.688 | <0.001 |
| | context (sympatry) | 0.309 | 0.251 | 1.230 | 0.219 |
| | robot ID (conspecific) | 0.833 | 0.251 | 3.315 | <0.001 |
| | context: robot ID | 0.832 | 0.393 | 2.118 | 0.034 |
| Push-up two legs and dewlapping | (Intercept) | -2.938 | 0.177 | -16.566 | <0.001 |
| | context (sympatry) | 0.251 | 0.251 | 0.998 | 0.318 |
| | robot ID (conspecific) | 0.609 | 0.251 | 2.421 | 0.016 |
| | context: robot ID | 0.871 | 0.394 | 2.211 | 0.027 |
| Push-up two legs | (Intercept) | -2.789 | 0.177 | -15.783 | <0.001 |
| | context (sympatry) | 0.220 | 0.251 | 0.875 | 0.382 |
| | robot ID (conspecific) | 0.638 | 0.251 | 2.539 | 0.011 |
| | context: robot ID | 0.856 | 0.393 | 2.178 | 0.029 |
| Push-up four legs and dewlapping | (Intercept) | -2.930 | 0.177 | -16.521 | <0.001 |
| | context (sympatry) | 0.257 | 0.251 | 1.024 | 0.306 |
| | robot ID (conspecific) | 0.860 | 0.251 | 3.425 | <0.001 |
| | context: robot ID | 0.696 | 0.393 | 1.771 | 0.077 |
| Push-up four legs | (Intercept) | -2.963 | 0.178 | -16.694 | <0.001 |
| | context (sympatry) | 0.299 | 0.251 | 1.189 | 0.234 |
| | robot ID (conspecific) | 0.557 | 0.252 | 2.216 | 0.027 |
| | context: robot ID | 0.719 | 0.394 | 1.825 | 0.068 |
| Tongue out | (Intercept) | -2.954 | 0.177 | -16.647 | <0.001 |
| | context (sympatry) | 0.272 | 0.251 | 1.081 | 0.280 |
| | robot ID (conspecific) | 0.811 | 0.251 | 3.228 | 0.001 |
| | context: robot ID | 0.810 | 0.393 | 2.060 | 0.039 |

in the time spent displaying crest erection, pati-pato, push-up two legs (with and without dewlapping) and tongue out behaviours towards conspecifics versus heterospecifics in sympatry compared to allopatry.

The potential costs of responding to heterospecific competitors (Lappin & Husak, 2005) might favour species-specific signals that discriminate conspecifics from heterospecifics (Bradbury & Vehrencamp, 2011) and a stronger response to the signals of the former (Ord & Stamps, 2009; Price, 2008) due to higher resource overlap (Peiman & Robinson, 2010). Conversely, species that evolved in

strict allopatry (such as isolated anole species in the Lesser Antilles) are expected not to discriminate conspecific from heterospecific signals due to the lack of selection pressure for species recognition (Clark et al., 2015). *Anolis oculatus* presents species-specific signals (i.e. display: Dufour et al., 2018a; and morphology: Dufour et al., 2018a; Dufour et al., 2018) and recognition (this study) allowing it to discriminate between conspecifics and *A. cristatellus*, despite having no common history with the invasive species (Losos, 2009). This result enriches the unexpected, yet significant list of examples of allopatric species who have been demonstrated to show species

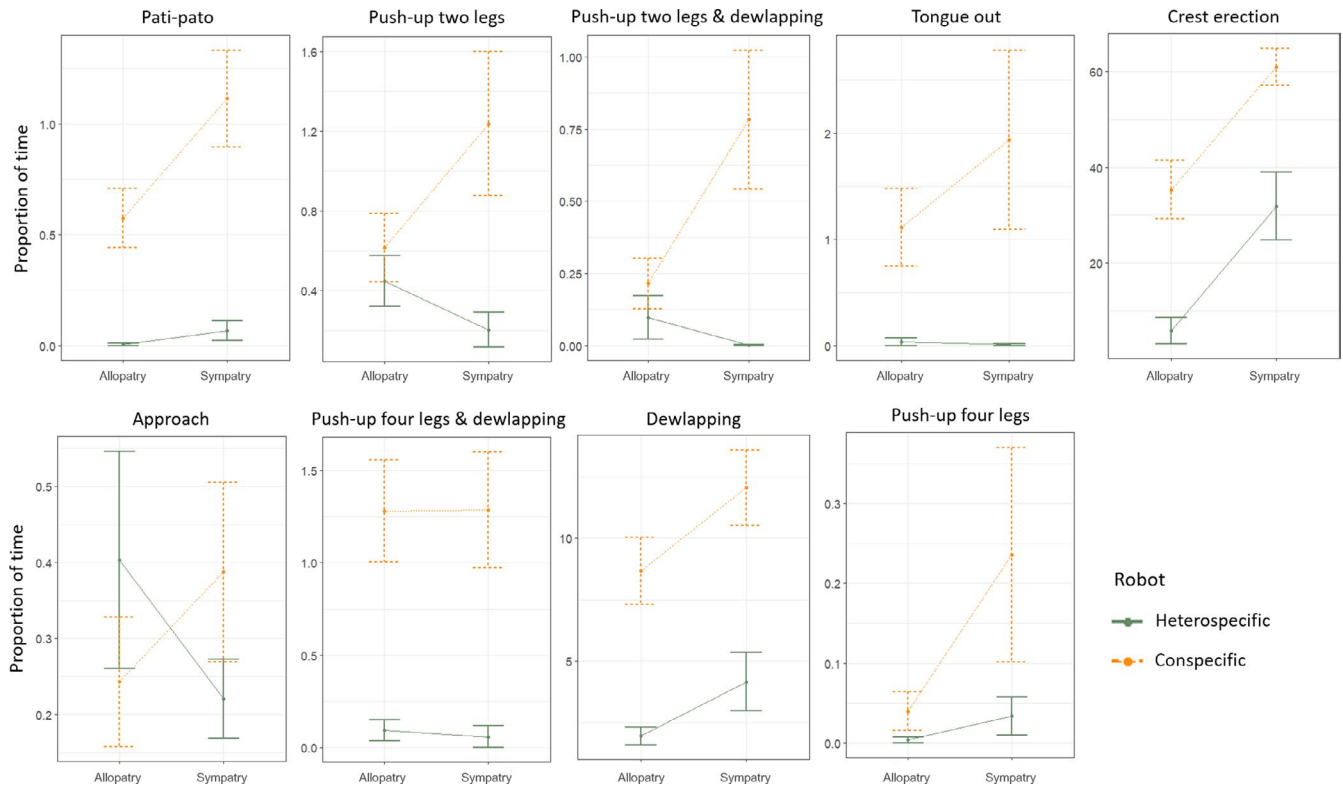


FIGURE 4 Percentage ($M \pm SE$) of the nine display behaviours performed by *Anolis oculatus* males towards conspecific and heterospecific robots in allopatry and sympatry

recognition (Ord, King, & Young, 2011). Hence, the behavioural response to conspecifics and heterospecifics appears to be less predictable than previously thought (Clark et al., 2015; Ord & Stamps, 2009), probably due to the plethora of potential factors involved in specific recognition (e.g. sexual selection, signal transmission properties of the environment, predation, parasitism, genetic and cultural shifts; Peiman & Robinson, 2010).

Although why *A. oculatus* responds differently to conspecifics versus heterospecifics remains unknown, the consequences of such species recognition in the coexistence outcome might be tangible. Indeed, when two species enter into contact, inherent species recognition would limit time and energetic expenses (Brandt, 2003) and risk of injury (Lappin & Husak, 2005) associated with irrelevant displays towards heterospecifics.

In addition to inherent species recognition, *A. oculatus* presents behavioural shifts in sympatry that might impact its coexistence with *A. cristatellus*. First, divergence in crest erection, pati-pato, push-up two legs (with and without dewlapping) and tongue out behaviours in *A. oculatus* towards conspecifics versus heterospecifics in sympatry could reflect changes meant to enhance species recognition. Such response divergence in sympatry may limit behavioural interference by, for example increasing the efficiency of the warning signal towards heterospecifics, and thus favour species coexistence. In a similar way, males of the poison dart frog *Allobates femoralis* present a more species-specific response when in sympatry with a closely related species, *Epipedobates trivittatus*, that calls at a similar but lower frequency than *A. femoralis* (Amezquita et al., 2006).

Second, the general increase of display response rate of *A. oculatus* reflects increased aggressiveness in sympatry. A growing body of evidence has demonstrated that the most aggressive species might expand its range and place constraints on geographic distribution and population size of closely related species competitors (Duckworth et al., 2015; Grether et al., 2017; Holway & Suarez, 1999; Jankowski, Robinson, & Levey, 2010; Pasch et al., 2013). For example, asymmetric aggressive interference linked to habitat changes lead to cyclic replacements of mountain bluebirds by western bluebirds in the United States (Duckworth et al., 2015). In Panama and Costa Rica, Pasch et al. (2013) revealed that aggressive dominance mediates altitudinal zonation in two species of neotropical singing mice. In Dominica, morphological (Dufour et al., 2018a), physiological (Dufour et al., 2018) and behavioural evidence (Dufour et al., 2018b) suggest that *A. oculatus* would be the dominant species during aggressive encounters with *A. cristatellus*. Increased aggressiveness would reinforce the species dominance of *A. oculatus* in sympatry and hence would provide an advantage to the native species during behavioural interference. Nonetheless, further studies on species dominance and aggressive interference are needed to determine the consequences of behavioural changes in *A. oculatus* on the coexistence between the native and invasive anole species in Dominica.

While the display shift of *A. oculatus* represents a clear-cut pattern, the causes underlying this behavioural changes remain unknown. Interspecific competition has been shown to drive such behavioural shifts in three ways. Agonistic interference

(Anderson & Grether, 2010; Grether et al., 2017), reproductive (Höbel & Gerhardt, 2003) and exploitative (resource use; Huber, León, Hendry, Bermingham, & Podos, 2007; Huber & Podos, 2006) competition between closely related species may drive changes in species recognition and display. Indeed, populations can respond to aggressive interspecific interference by shifting phenotypically in traits that affect the rate, intensity or outcome of interspecific aggression (Anderson & Grether, 2010; Grether et al., 2013, 2017; Grether, Losin, Anderson, & Okamoto, 2009). While the shifts in encounter rates, species recognition and fighting ability in sympatry have been often observed, the demonstration of the causes of the aggressive interference has been missing in the majority of the cases (Grether et al., 2009). In Dominica, direct aggressive encounters between *A. oculatus* and *A. cristatellus* males have been observed and might be the potential drivers of behavioural shifts in the display of the invasive species (Dufour et al., 2018b). Alternatively, interspecific mating might drive display divergence in sympatry to avoid the production of hybrids (Höbel & Gerhardt, 2003). In Dominica, mating attempts between the native and invasive anole species have been observed in the field (C.M.S. Dufour, pers. obs.), yet the evolutionary impacts of such events are unknown. Finally, environmental changes in terms of signal transmission properties might drive shifts in species recognition, signal and display (Boughman, 2002; Endler & Basolo, 1998). In anoles in particular, microhabitat use (e.g. brightness and movement of the visual background) has been shown to be an important driver shaping communication (Leal & Fleishman, 2002; Ord, Peters, Clucas, & Stamps, 2007; Ord, Stamps, & Losos, 2010). In Dominica, interspecific competition led *A. oculatus* to move upwards on the trees in sympatry (Dufour et al., 2018a). While the habitat characteristics (i.e. canopy cover, habitat openness) appeared not to change with perch height (Dufour et al., 2018b), the latter might be correlated with a difference in visual background which might drive the display changes in sympatry.

An alternative possibility to species interactions is that environmental differences between allopatric and sympatric sites are responsible for the behavioural display shifts observed. Habitat structure, predation pressure and social context have been shown to be important drivers shaping communication behaviour in *Anolis* lizards (Leal & Rodriguez-Robles, 1995, 1997; Ord et al., 2007, 2010; Stamps, 1983). In this study we selected the sites to minimize habitat and predation differences between the two contexts by sampling the lizards in standardized banana farms. Habitat structure (i.e. openness) has been shown not to be different between the allopatric and sympatric sites sampled in Calibishie (Dufour et al., 2018b). Moreover, we did not observe qualitative differences in predation pressure between allopatric and sympatric sites in terms of number and type of predators observed (e.g. *Ameiva* lizards, birds, snakes, cats) and predation injuries recorded (pers. obs.). Population density is known to have strong effect of male competition and hence on the visual display in anoles (Stamps, 1983). Specifically, a higher anole population density is expected to lead to more displays to defend a territory and to attract females (Bloch & Irschick, 2006). However, the contrary pattern was observed in this study, with more displays

being observed in sympatric sites where density appears to be lower (both *A. oculatus* and total anole densities, Supplementary Material 2), which suggests that density is an unlikely driver of the display shift observed in the native species. Finally, while the apparent inland versus coastal spatial distribution of the allopatric and sympatric sites are neither correlated with anthropic activity (all the sites are within the village) nor with the environmental factors discussed above, it is always possible (yet unlikely) that other (unknown) factors might lead to potential differences in sites characteristics.

Thus, neither habitat structure, predation pressure, spatial distribution, nor population density appear to be strong candidates to explain the shift in display behaviour observed in the native species. The one factor that seems strongly associated with behavioural differences is the presence of *A. cristatellus* which is likely driving the shifts in species recognition and aggressive behaviour of *A. oculatus*. Yet the cause(s) (interference and exploitative competition) and process(es) (genetic basis, plasticity, learning) of such changes remain unknown. Nonetheless, the short distances between the sites sampled in Calibishie might not prohibit individuals from moving from one population to another, arguing in favour of behavioural plasticity and learning processes, rather than genetic differentiation, as the explanation of the shift in display behaviour of *A. oculatus*.

This rapid behavioural response might, in turn, have profound consequences on the competition outcome at the early stages of this biological invasion. For instance, native Californian ants were displaced by the invasive Argentine ant due to adaptations of the aggressive behaviour of the invasive species (Holway, 1999; Holway & Suarez, 1999; Human & Gordon, 1999). In Dominica, the lower *A. oculatus* population density observed in sympatry suggests a negative impact of *A. cristatellus* on the native species (Supplementary Material 2). Nonetheless, added to the morphological and physiological advantage of the native species (Dufour et al., 2018), species-recognition and increase in aggressive behaviour of *A. oculatus* in sympatry may favour the native species during aggressive interference with *A. cristatellus*.

To conclude, given rapid biodiversity decline, notably due to global change and biological invasions, it is particularly timely to focus on the importance of the behavioural components of recent interspecific interactions on population density, fitness and ecological forecasting. An accurate vision of the native-invasive species interaction outcome can be reached only if the behavioural piece is included in the puzzle.

ACKNOWLEDGEMENTS

We thank Inbar Maayan for her precious assistance in the field and Susanne Csmarich and Wendy Marcellin for their support in Calibishie. We thank Joe Macedonia for assistance creating DAP graphs shown in Figure 1. This study was performed thanks to a Putnam grant and a Fysen Foundation fellowship. This study was performed under the research permit from the Ministry of Agriculture and Fisheries, Forestry, Wildlife and Parks division of Dominica and with IACUC (no. 26-11) authorization from Harvard University.

AUTHORS' CONTRIBUTIONS

C.M.S.D. conceived and designed the experiments, performed the experiments, analysed the data, contributed reagents/materials/analysis tools, prepared figures and tables, authored and reviewed drafts of the paper, approved the final draft; D.L.C., A.H. and J.B.L. conceived and designed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper, approved the final draft.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5x69p8d0s> (Dufour, Clark, Herrel, & Losos, 2020).

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SUPPORTING INFORMATION

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

How to cite this article: Dufour CMS, Clark DL, Herrel A, Losos JB. Recent biological invasion shapes species recognition and aggressive behaviour in a native species: A behavioural experiment using robots in the field. *J Anim Ecol*. 2020;00:1–11. <https://doi.org/10.1111/1365-2656.13223>