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Is naïveté forever? Alien predator and aggressor recognition by two endemic island reptiles

A. Gérard · H. Jourdan · C. Cugnière · A. Millon · E. Vidal

Abstract The disproportionate impacts of invasive predators are often attributed to the naïveté (i.e., inefficient or non-existing anti-predator behavior) of island native species having evolved without such predators. Naïveté has long been regarded as a fixed characteristic, but a few recent studies indicate a capacity for behavioral adaptation in native species in contact with alien predators. Here, we tested whether two reptiles endemic to New Caledonia, a skink, *Caledoniscincus austrocaledonicus*, and a gecko, *Bavayia septuiclavis*, recognized and responded to the odor of six introduced species (two rodents, the feral cat, and three species of ants). We used an experimental design in which reptiles had a choice of retreat sites with or without the odor of predators or aggressors. Skinks avoided two or three of the predators, whereas geckos avoided at most one. These results suggest that diurnal skinks are more responsive than nocturnal geckos to the odor of introduced predators. Neither skinks nor geckos avoided the three species of ants. Thus, the odors of alien predators are shown to influence retreat site selection by two native island reptiles. Moreover, the study suggests that this loss of naïveté varies among native species, probably as a consequence of the intensity of the threat and of time since introduction. These findings argue for re-thinking the behavioral flexibility of

ectothermic reptiles in terms of their responses to biological invasion.

Keywords Naïveté · Anti-predator response · Retreat site selection · Invasive species · Behavioral adaptation

Introduction

Biological invasions have been recognized as the major cause of species extinction on islands (Vitousek et al. 1997). The dramatic impact of alien predators on native insular species has been mainly attributed to island prey naïveté (Carthey and Banks 2012). Ecological naïveté can be defined as ineffective anti-predator defenses due to the absence of a shared evolutionary history with predators (Cox and Lima 2006). Not all naïve prey, however, show ineffective anti-predator responses to novel predators (Sih et al. 2010). Carthey and Banks (2014) classified naïveté into four categories: (i) prey types which show no recognition of the alien species as a predator; (ii) prey types recognizing the predator as dangerous but adopting the wrong anti-predator response; (iii) prey types recognizing the predator as dangerous, having an appropriate anti-predator response but being “outgunned” by the superior tactics of the alien species; and (iv) prey types responding appropriately and effectively, but over-allocating effort to this response beyond what is necessary to minimize lethal effects. The progression through the multiple levels of naïveté towards predator wariness should occur with sufficient experience and passage of time (Banks and Dickman 2007). Therefore, time since introduction of a novel predator could be one factor in this gradual shedding of naïveté. Evolutionary theory predicts that prey must either adapt to new threats or become extinct (Schlappfer et al. 2005; Carthey and Banks 2012). To date, behavioral changes in native prey facing alien predators have only rarely been demonstrated, in some amphibian

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(Kiesecker and Blaustein 1997), fish (Pollock et al. 2003), and island mammal species (Russell and Banks 2007; Carthey and Banks 2012) but there has been little examination of the ability of reptilian species to develop anti-predator responses (but see Freidenfelds et al. 2012; Li et al. 2014).

Island reptiles are known to be highly vulnerable to alien predators (mongooses, cats, rodents) or aggressive invaders (e.g., fire ants) (Case and Bolger 1991; Towns et al. 2001; Gasc et al. 2010; Freidenfelds et al. 2012). However, recent studies using native predator species (i.e., snake species), or where an investigator approaches in such a way as to simulate predation risk, reveal that island reptile species have a capacity for behavioral adaptation, i.e., changes in activity and mobility, adaptive vigilance, wariness, and flight distance (Downes 2002; Berger et al. 2007; Placyk and Burghardt 2011). Anti-predator behaviors were shown to differ across populations depending on whether or not they had previously been exposed to introduced predators or on whether or not populations were syntopic with native predators (Downes 2002; Placyk and Burghardt 2011).

Reptiles used vomerolfaction, a sense similar to olfaction but with distinct epithelium and neural connections (Cooper and Burghardt 1990), and olfactory cues to detect prey, predators, or aggressors (Cooper and Alberts 1991; Dial and Schwenk 1996; Goldsbrough et al. 2006). One technique commonly exploited to study the perceived risk of predation is to use the odors of the feces and/or urine of predators (Hayes 2008). Four studies showed that the odor of native predators (snakes or varanid species) influences retreat site selection by skinks and geckos (Downes and Shine 1998a, b; Stapley 2003; Lloyd et al. 2009). Retreat site choice experiments mimic situations that reptiles experience in their natural habitat (i.e., retreat into small crevices) and that allow them to reduce their vulnerability to predators (Schlesinger and Shine 1994).

Here, we tested whether two island endemic reptiles (a diurnal skink and a nocturnal diplodactylid gecko) recognize and respond to the odor of a range of alien predators and aggressors, using a retreat site choice experiment. Loss of naïveté was expected to vary depending both on the ecology of these two reptile species and on the impact and/or the time since introduction of the alien species.

Methods

Study species

Behavioral experiments were conducted on two common wild reptile species endemic to New Caledonia, the common litter skink (*Caledoniscincus austrocaledonicus*) and the pale-striped Bavayia gecko (*Bavayia septuiclavis*). Skinks are diurnal species widespread in the litter of both open and wooded

habitats on the west coast of the main island, whereas geckos are nocturnal and arboreal species inhabiting the closed humid forest of the south (Bauer and Sadlier 2000).

Successive waves of human colonization of New Caledonia brought numerous alien species that have subsequently become invasive. The predators we focused on here were (i) the Pacific rat (*Rattus exulans*) introduced by the first Melanesian settlers ca. 3,000 years ago (Pascal et al. 2006), (ii) the ship rat (*Rattus rattus*), and (iii) the feral cat (*Felis catus*), the two latter species having arrived in New Caledonia in the nineteenth century with European colonizers (Pascal et al. 2006). An ongoing study in New Caledonia finds skinks and geckos to be common prey in feral cat and rat diets (IMBE, unpublished data).

The aggressors we tested were three of the four introduced species of ants considered the most invasive in New Caledonia (Jourdan and Mille 2006): the little fire ant (*Wasmannia auropunctata*), the tropical fire ant (*Solenopsis geminata*), and the big-headed ant (*Pheidole megacephala*), which were introduced into New Caledonia between 1881 and 1964 (Jourdan and Mille 2006). These three species have a negative impact on both species richness and abundance of lizards (Jourdan et al. 2001; Wojcik et al. 2001; Fisher and Ineich 2012).

Reptiles were collected by hand in the field (then released after experiment) from the south of the main island in areas invaded by alien mammal predators (Pacific and ship rat, feral cat) and aggressors (invasive ants). For skinks, each individual was captured several hours before the experiment and placed in a small plastic box with a few leaves and water ad libitum 1 h before the beginning of the experiment. For geckos, each individual was maintained in a small plastic box with a few leaves, a piece of wood, crickets, and water ad libitum before and between experiments.

Retreat site choice experiment

We tested reptile response to the odor of alien species through retreat site choice (Downes and Shine 1998b; Stapley 2003). Retreat site choice has been used successfully in previous studies to assess the avoidance behaviors of lizards and provides a robust measure of predator avoidance (Stapley 2003; Lloyd et al. 2009). Tests were conducted after sunset for diurnal skinks and after sunrise for nocturnal geckos, respectively, during the normal activity period of these two species. Lizards were placed in opaque plastic boxes ($l \times w \times h$: $32 \times 21 \times 20$ cm) containing two ceramic tiles (7×7 cm) as retreat sites (Fig. 1). Boxes and tiles were washed with 95 % alcohol and dried between trials, and all manipulations were performed wearing latex gloves, to avoid human odor. A paper towel was placed under each tile, one treated with odors (predators, aggressors, or scent control) the other with distilled water (odorless control). To distinguish whether responses to

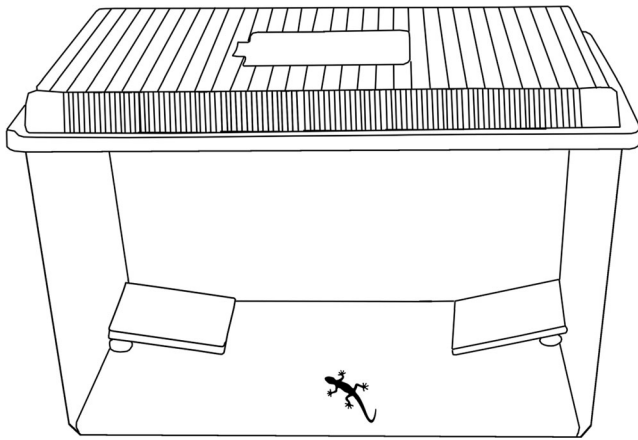


Fig. 1 Experimental design. Skinks or geckos are individually placed at the center of the front part of the box at the beginning of the experiment (GNU Image Manipulation Program 2.8)

odor were specific to the odor of predators or aggressors, or simply responses to any odor, we used as control scent a biological odor outside the experience of the species and the individuals tested (Dial and Schwenk 1996). With our reptile populations not being coastal, we chose the odor of a seabird (wedge-tailed shearwater *Puffinus pacificus*) as a non-predator, biological, odorous but unfamiliar odor. Cologne is sometimes used in tests of chemoreception in squamates (Cooper 1995a; Dial and Schwenk 1996; Amo et al. 2004) but Dial and Schwenk (1996) suggested it is not an appropriate control scent because it may act as an irritant and suppress some chemosensory behavior. Choice and position of odor (right or left) were randomly determined before each trial (Stapley 2003; Lloyd et al. 2009). Responses were measured by comparing avoidance ratings defined as the number of odorless control tile choices divided by total number of tile choices.

Preliminary tests on 30 individuals per species showed that the response rate (i.e., the total number of tile choices (odorless control and scented tiles) divided by the total number of tests) for skinks decreased from 76 % when confronted with the first odor to 43 % when confronted with the last odor, while it was systematically high (87.2 ± 5 %) for geckos (Fig. 2). To avoid this undesirable non-response effect, we confronted each skink with one odor only, while each gecko was successively confronted with all the odors in random order. We determined that odor sequence did not influence gecko retreat site choice (generalized linear mixed models (GLMM); $P=0.93$). Tests were therefore performed on 514 adult skinks and 53 adult geckos, and we obtained a response rate of 67 ± 13 % for skinks and 80.4 ± 6.1 % for geckos. Only responding lizards, those that had chosen a retreat site by the end of the experiment, were included in the calculation of the avoidance rating. The non-responding lizards, those that remained outside the tiles and did not choose a retreat site, were excluded from the calculation of the avoidance rating.

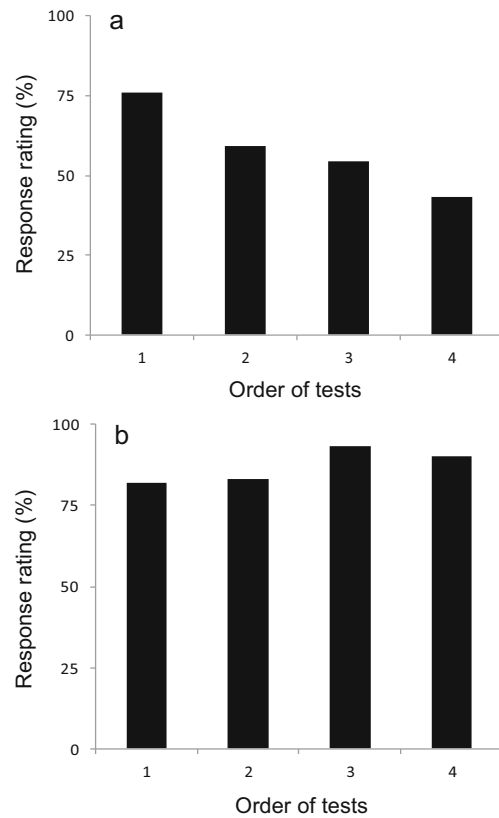


Fig. 2 Response rating (i.e. total number of tile choices divided by total number of tests) for **a** skinks ($n=30$) and **b** geckos ($n=30$) when each individual tested all odors in random order

The odor of rats was obtained by placing paper towels on the floor of cages containing wild-trapped rats to collect urine and feces (Head et al. 2002). The odor of cats was obtained by placing paper towels on the fur of a cat caught at capture sites and crushing feces on these paper towels. The odors of *P. megacephala*, *S. geminata*, and *W. auropunctata* were obtained by crushing the ants on paper towels placed at the bottom of boxes where the ants were kept for several days before testing. The control scent was obtained by placing paper towels on fresh corpses of *P. pacificus*.

We video-recorded the first 17 tests on skinks over 3 h. Analysis of the videos showed that 16 out of 17 lizards made their final choice of tile within the first 2 h, so we set test duration at 2 h. The tile under which the lizards were hiding at the end of testing was arguably representative of their choice, since a further 54 tests on skinks and 30 on geckos showed that skinks spent the last 82 ± 8 min under the final tile and geckos the last 112 ± 13 min.

Data analysis

We tested whether skinks and geckos avoided a control scent (i.e., the odor of *P. pacificus*) unrelated to any predator/aggressor. Then, we compared lizard avoidance scores when

confronted with predator or aggressor odors according to two different control references: (i) no effect of odor (i.e., random choice corresponding to an avoidance rating at 50 %) and (ii) control scent (*P. pacificus* odor). These two ways of analyzing the data yield complementary information: the first one revealing whether a particular predator/aggressor odor is attractive/repulsive and the second revealing whether one particular predator/aggressor odor is more attractive/repulsive than an unknown odor unrelated to any predator/aggressor. Doing this comparison would allow us to tease apart the strategy “avoid any odor” from “avoid the odor of recognized predator.” Statistical analyses were performed using generalized linear models (GLM) for skinks and generalized linear mixed models (GLMM) for geckos, with individual identity as a random factor to control for replicated data coming from a same individual. We also added sequence

(order of odor presentation) as a fixed factor in the analysis for geckos. Both models were fitted with a binomial distribution of error (with logit link) and were implemented in R 2.15.0 (R Development Core Team 2012) using the “lme4” library (Bates et al. 2014).

Results

Neither skinks nor geckos showed any avoidance of the control scent ($P=0.65$; $P=0.12$, respectively) (Fig. 3; Table 1), indicating that they are not simply avoiding any scent, but are specifically responding to the scent of predators.

Our models showed that diurnal skinks were more responsive than nocturnal geckos whatever the intercept considered. In fact,

Fig. 3 Avoidance rating (number of control tile choices divided by total number of tile choices) for: (1) skinks for retreat sites treated with the odor of control scent and predator; (2) geckos for retreat sites treated with the odor of control scent and predator; (3) skinks for retreat sites treated with the odor of control scent and aggressor; and (4) geckos for retreat sites treated with the odor of control scent and aggressor. Significance levels are indicated by letters above the bars (*a* significantly different from 50 %, the reference represented by the dotted line; *b* significantly different from control scent)

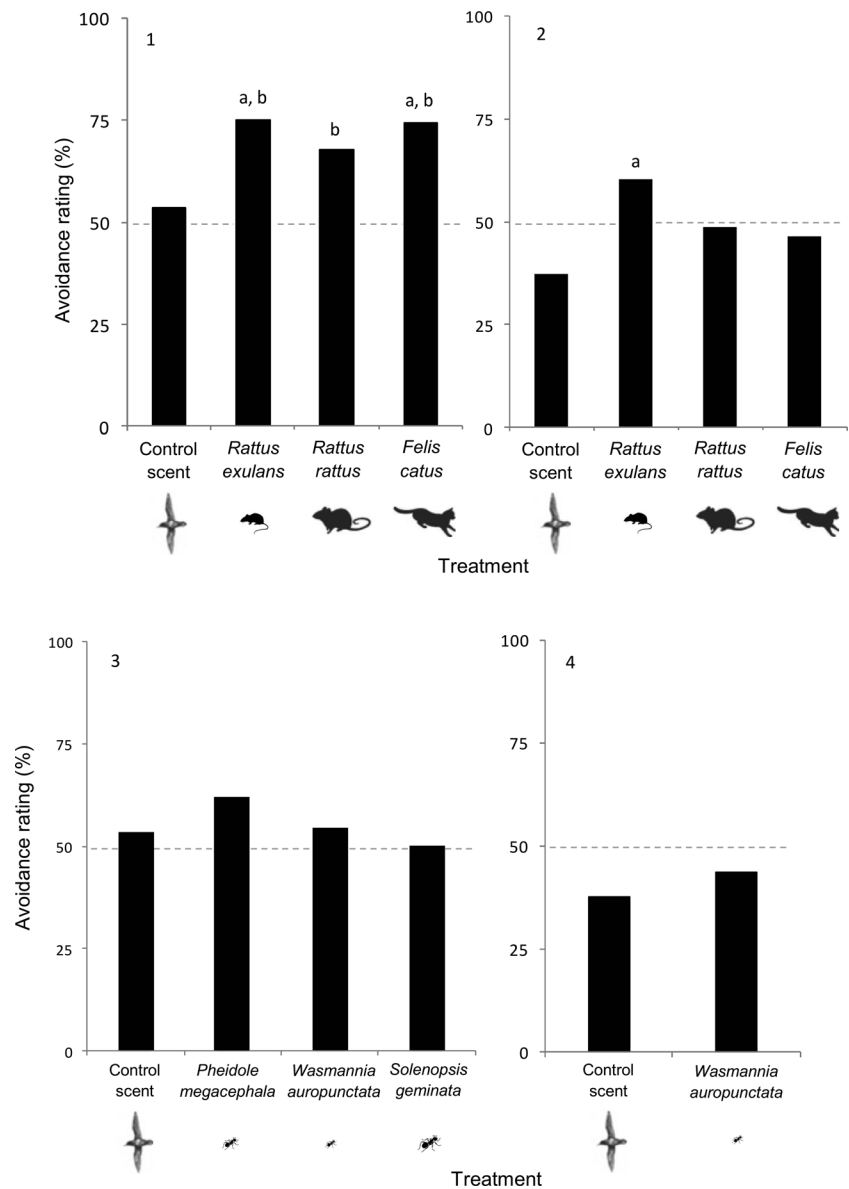


Table 1 Results of GLM for (a) skinks for tests with the odor of predator and skinks for tests with the odor of aggressor and LMER for (b) geckos for tests with the odor of predator and geckos for tests with the odor of aggressor, with no effect of odor (i.e. fixed avoidance rate at 50 %) as the intercept

	Estimate	Standard error	Pr(> z)
a			
Control scent	0.133	0.299	0.655
<i>R. exulans</i>	1.099	0.333	0.001
<i>R. rattus</i>	0.747	0.286	0.009
<i>F. catus</i>	1.068	0.349	0.002
Control scent	0.133	0.299	0.655
<i>P. megacephala</i>	0.480	0.353	0.174
<i>W. auropunctata</i>	0.182	0.350	0.602
<i>S. geminata</i>	0.000	0.324	1.000
b			
Control scent	-0.523	0.334	0.118
<i>R. exulans</i>	0.425	0.312	0.173
<i>R. rattus</i>	-0.049	0.312	0.876
<i>F. catus</i>	-0.147	0.313	0.640
Control scent	-0.531	0.339	0.117
<i>W. auropunctata</i>	-0.259	0.323	0.425

skinks avoided either two (i.e., the Pacific rat and the feral cat; $P < 0.04$; Fig. 3 1; Table 2 a) or all three of the predator odors tested (i.e., the Pacific rat, the black rat, and the feral cat; $P < 0.009$; Fig. 3 1; Table 1 a) depending on the intercept. By

Table 2 Results of GLM for (a) skinks for tests with the odor of predator and skinks for tests with the odor of aggressor and LMER for (b) geckos for tests with the odor of predator and geckos for tests with the odor of aggressor, with control scent (*P. pacificus*) as the intercept

	Estimate	Standard error	Pr(> z)
a			
Control scent	0.133	0.299	0.655
<i>R. exulans</i>	0.965	0.448	0.031
<i>R. rattus</i>	0.614	0.414	0.138
<i>F. catus</i>	0.934	0.460	0.042
Control scent	0.133	0.299	0.655
<i>P. megacephala</i>	0.346	0.462	0.454
<i>W. auropunctata</i>	0.049	0.460	0.916
<i>S. geminata</i>	-0.133	0.441	0.762
b			
Control scent	-0.523	0.334	0.118
<i>R. exulans</i>	0.958	0.454	0.035
<i>R. rattus</i>	0.464	0.454	0.307
<i>F. catus</i>	0.377	0.455	0.407
Control scent	-0.531	0.339	0.117
<i>W. auropunctata</i>	0.261	0.473	0.581

contrast, geckos avoided the Pacific rat alone when compared with the control scent alone ($P = 0.03$; Fig. 3 2; Table 2 b).

The Pacific rat was therefore the only predator avoided both by skinks and by geckos ($P < 0.03$; $P = 0.03$ respectively; Fig. 3 1, 2; Tables 1 and 2), the feral cat and the ship rat being avoided only by skinks ($P < 0.04$; Fig. 3 1; Table 1).

No avoidance by either lizard could be detected for the odor of the three invasive ants tested ($P > 0.05$; Fig. 3 3, 4; Tables 1 and 2) whatever the intercept considered.

Discussion

Some island gecko or skink species are known to be able to detect and avoid the scent of native predators (Downes and Shine 1998b; Stapley 2003; Lloyd et al. 2009), but this has never been tested for the scent of non-native predators. Here, a diurnal lizard species, and to a lesser extent a nocturnal gecko, were proved to recognize and avoid the scent of some alien predators.

The difference in avoidance observed between skinks and geckos suggests that each pair of antagonistic species, i.e., one endemic prey vs one introduced predator, should be considered separately. One reason for this difference might originate in the distinct ecology of the two reptile species. Skinks are diurnal species spending most of their time in retreat sites at night, when the three predators considered here are the most active. In contrast, geckos are nocturnal species occupying retreat sites during the day, when the three predators are less active. Therefore, the selection of a retreat site without predator odor would appear to be more crucial for skinks than for geckos. Moreover, skinks are active foragers making good use of their prey chemical discrimination abilities, whereas geckos tend to be ambush foragers relying less on prey chemical discrimination (Cooper 1995b). This could explain why the avoidance of the odor of predators was less pronounced for geckos than for skinks.

Length of time since introduction could also be considered as a possible factor in loss of naïveté (Banks and Dickman 2007). Here, the only predator avoided by both skinks and geckos was the Pacific rat, which was the earliest introduced predator. Thus, after ca. 3,000 years of co-existence with Pacific rats, skinks and geckos apparently associated the odor of the Pacific rat with a threat. However, despite a more recent introduction, the ship rat and the feral cat were already avoided by skinks. This implies that avoidance behavior may also depend on other factors, especially the archetype of the novel predator (Carthey and Banks 2014) and the level of predation risk (Stapley 2003; Lloyd et al. 2009).

It has also been suggested that similar responses towards the odors of different predator species may be due to similarities in the chemical composition of these odors (Hayes 2008). As the ship rat belongs to the same predator threat type as the Pacific rat (Cox and Lima 2006), the long-standing presence of Pacific rats

could have “prepared” endemic skinks to avoid the more recently introduced ship rats.

Moreover, strength of predator-prey interaction (i.e., level of predation risk) could also influence avoidance behavior (Stapley 2003; Lloyd et al. 2009). In fact, a more recently introduced predator with major impact could evoke a greater prey response than an older introduced predator with less impact. Previous studies showed that some island gecko or skink species prioritize avoidance of predators posing different levels of threat (Stapley 2003; Lloyd et al. 2009). Recent diet studies conducted in New Caledonia (unpublished data) show that reptiles are less frequent in the ship rat diet than in the Pacific rat diet and that geckos are significantly less frequent in the feral cat diet than skinks (though the relative abundance of the two lizards are unknown). Developing anti-predator behavior is costly for prey species and is likely only if the costs are outweighed by the benefits (Blumstein and Daniel 2005; Lloyd et al. 2009). The intensity of the threat could thus be a key factor shaping anti-predator behavior leading to a loss of naïveté in native prey.

Both length of time since introduction and intensity of threat could explain why the two reptile species failed to respond to the odor of invasive ants, even though invasive ants are noxious aggressors known to reduce both the species richness and the abundance of reptiles (Wojcik et al. 2001; Jourdan and Mille 2006; Fisher and Ineich 2012). Invasive ants are the most recently introduced species, and their ca. 50–130 years of co-existence could be too short to induce the development of behavioral adaptations. It has been shown that a common evolutionary history between ants and lizards allows an Australian skink to detect native ants based on chemosensory cues (Goldsbrough et al. 2006). During fieldwork, Goldsbrough et al. (2006) rarely found this lizard under rocks with ants, but in experimental trials, the lizard did not avoid ant-scented retreat sites. Therefore, another hypothesis is that ant olfactory cues alone may be insufficient to induce avoidance of a retreat site, even though previous studies have already demonstrated that physical contact between invasive ants and reptiles can cause behavioral changes (Langkilde 2010; Freidenfelds et al. 2012). In addition, body size and ontogenetic variation in anti-predator behavior (i.e., lower running speed and shorter flight distance) could make juvenile lizards more vulnerable to predation (Martin and Lopez 2003). In our study, therefore, a lower risk of predation on adults could explain their lack of avoidance of the odor of invasive ants.

Our findings support the hypothesis that endemic island reptile species can indeed lose their original naïveté, learning and adapting to new threats such as introduced predators. This is in agreement with the idea put forward by Carthey and Banks (2012) that the behavioral flexibility of some prey indicates that the “alien” status should not be considered immutable, i.e., that naïveté of island prey is not necessarily

permanent and unalterable. Carthey and Banks (2012) propose that introduced species should be considered as native when the recipient community adapts to their novelty (e.g., when native prey develop appropriate anti-predator behavior). Further studies are required to determine whether the recipient community has really adapted to these new predators, but our findings suggest that this process may have begun for the two lizard species considered here. The mechanisms underlying the establishment of anti-predator behavior remain to be tested but such responses have been found to result from both innate factors and postnatal experience for snake species (Weldon 1982; Weldon and Burghardt 1979).

In conclusion, the capacity of some prey species to develop adaptive anti-predator behaviors (e.g., avoidance of scent marks of their predators) reduces the probability of encountering the predator and facilitates the co-existence of native prey and alien predators (Russell and Banks 2007; Hayes 2008). Thus, understanding the interactions between alien and native species in the mid to long term after establishment is crucial if management strategies for long-established invaders are to be designed (Strayer et al. 2006). Such adaptive behavior also argues for prioritizing eradication or control of the more recent invaders because of their intensive impacts.

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Ethical standards The experiments comply with the current laws of France and New Caledonia (permission for sampling protocol (decreen 2155-2012/ARR/DENV)).

Conflict of interest The authors declare that they have no conflict of interest.

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