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# Anti-predator behaviour changes following an aggressive encounter in the lizard *Tropidurus hispidus*

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Avoiding predators may conflict with territorial defence because a hiding territorial resident is unable to monitor its territory or defend it from conspecific intrusions. With persistent intruders, the presence of an intruder in the near past can indicate an increased probability of future intrusions. Therefore, following a conspecific intrusion, territorial residents should minimize costs from future intrusions at the cost of higher predation risks. I conducted experiments with males of the territorial lizard *Tropidurus hispidus* recording approach distance (distance between predator and prey when the prey escapes) and time to re-emergence from a refuge after hiding. Past aggressive interactions affected anti-predator behaviour: lizards re-emerged sooner (compared to a control) when the predator attacked 5 min after an aggressive encounter. If the predator attacked while an aggressive encounter was ongoing, there was also a reduction in approach distance. The results are consistent with an economic hypothesis which predicts that *T. hispidus* incur greater predation risks to minimize future territorial intrusion; additionally they show that the effects of past and ongoing aggressive interactions are different, consistent with the minimization of present intrusion costs. These results are relevant for studies of the changes in aggressive behaviour due to changes in the social environment and for studies of the costs and (co)evolution of aggressive and anti-predator strategies.

**Keywords:** anti-predator behaviour; predation risk; aggressive behaviour; territoriality; trade-off;  
*Tropidurus hispidus*

## 1. INTRODUCTION

Optimal anti-predator behaviour should be the result of weighing the risk of predation against the benefits from other activities. Experimental and theoretical work, focused mainly on the trade-off between foraging and predator avoidance, has shown that changes in terms of the trade-off between the mortality risk from predation and costs of hiding and/or escaping from predators will change the behavioural optimum (see Ydenberg & Dill 1986; Clark 1994; see the reviews in Lima & Dill 1990; Lima 1998). Thus, when the costs of interrupting other activities increase (e.g. foraging at a better patch or consuming larger prey), animals adopt behavioural strategies which lead to increases in the risk of mortality from predation (e.g. delaying escape from a predator or re-emerging from a refuge sooner). In territorial animals, territorial defence can be an important determinant of reproductive success. However, compared to the anti-predator–foraging trade-off, there is little information about trade-offs between anti-predator behaviour and territorial defence. The general aim of this study was to examine how predation-related risk-taking behaviour changes as a consequence of past and present aggressive interactions which increase the territorial costs of hiding; the two hypotheses tested predict increased exposure to predation as a consequence of the increased costs of

hiding due to past (first hypothesis) or present (second hypothesis) territorial conspecific intrusions.

A predatory attack creates conflicting demands on a territorial animal: hiding decreases the risk of mortality from predation, but minimizes the chances of detecting and repelling a conspecific intruder (i.e. it increases the territorial costs of hiding). These territorial costs of hiding can be particularly high following a conspecific intrusion: in some territorial species intruders obtain or enlarge territories by persistently intruding into the territories of settled animals (see the reviews in Stamps & Krishnan (1995, 1998)), e.g. the lizard *Anolis aeneus* (Stamps & Krishnan 1995), red-winged blackbirds (Yasukawa 1979), purple martins (Stutchbury 1991) and song sparrows (Arcese 1987). Thus, the occurrence of one aggressive encounter can inform a territorial resident that subsequent territorial intrusions are likely.

The first hypothesis tested in this study states that a past territorial intrusion changes the terms of the trade-off between predation and vigilance by increasing the territorial costs of hiding and, thus, alters the behavioural optimum. Therefore, if a predator attacks soon after an aggressive interaction is over, a territorial resident should modify its behaviour to decrease the chances of territorial intrusions at the cost of increased predation risks (hereafter called the extended effects of aggression on anti-predator behaviour). The predictions from this hypothesis

are that, following an aggressive encounter, a territorial resident will show a decrease in the distance at which it flees from a predator and/or a decrease in the time until it re-emerges from a refuge after the predator attacks. These predictions were tested in experiment 1 using a human as a simulated predator and comparing the anti-predator behaviour in males of the lizard *Tropidurus hispidus* 5 min after the end of an aggressive interaction with anti-predator behaviour 5 min after a control presentation.

The anti-predator behaviour consequences of a change in the territorial costs of hiding can be studied further by examining the difference between the effects of an aggressive encounter that has finished (extended effects) and an ongoing aggressive interaction (immediate effects). In an ongoing aggressive encounter the intruder is in the territory when the predator attacks and hiding could result in much larger intrusion costs, particularly if the approaching predator is not an attacking one. The second hypothesis tested in this paper states that the current presence of an intruder increases the territorial costs of hiding with respect to the past presence of an intruder and, thus, that territorial residents should show further increases in their exposure to predation when the predator approaches during an ongoing aggressive encounter versus some time after the end of the aggressive interaction. This hypothesis predicts that the immediate effects will result in a decrease in the distance at which the territorial resident flees from a predator and/or a decrease in the time until it re-emerges from a refuge after the predator attacks compared to the extended effects. I examined this hypothesis in experiment 2 by comparing the anti-predator behaviour of male *T. hispidus* during an ongoing aggressive encounter with anti-predator behaviour 5 min after the end of the aggressive interaction.

## 2. METHODS

### (a) *Animals and study site*

The experiments (table 1) were conducted at the Nisia Floresta Forest Experimental Station, EFLEX-IBAMA (6°5'S, 35°12'W), located 45 km from Natal (north-eastern Brazil). Experiment 1 was conducted between 27 April and 22 May 1997 and experiment 2 between 29 November 1997 and 13 January 1998. I used adult males of the lizard *T. hispidus* (snout-vent length (SVL), 70–130 mm), a widespread, diurnal, sit-and-wait iguanine lizard in South America (Rodrigues 1987; Vitt 1995). In the area studied both male and females were territorial throughout the year and encounters between males which developed into escalated fights tended to repeat themselves (with the same contenders) in subsequent hours or days (R. Díaz-Uriarte, personal observation).

The experimental subjects were adult males (SVL ≥ 100 mm), captured in villages close to the station, which had not been used in other experiments or used before as intruders or later used as intruders in the same enclosure. Intruders (adult males SVL > 90 mm) were used a maximum of three times and were never wounded by the experimental procedure. The same experimental animal was not exposed to the same intruder more than once. Intruders were assigned at random to experimental animals, but no intruder could be used twice in the same enclosure and for the same treatment (in experiment 2). Moreover, for each experimental animal in experiment 2, none of the two treatments could be applied using either the two largest or

the two smallest intruders to ensure adequate interspersions with respect to the intruders' sizes (this is not applicable in experiment 1 where each experimental animal was subject to only one intruder). All animals were released in the area of capture at the end of testing.

### (b) *Enclosures and animal husbandry*

I used enclosures to minimize variation in behaviour. The enclosures were located in open patches in plantation areas and measured 3.6–4.9 m<sup>2</sup> (2–2.5 m × 2 m) in experiment 1 and 4 m<sup>2</sup> (2 m × 2 m) in experiment 2. The enclosures were 1 m high, constructed from transparent plastic, sunk 15 cm into the ground and attached to a wood frame. Each enclosure contained two refuges made with bricks and roof tiles which offered protection and were readily used by the lizards as hiding places. The enclosures were partially covered from above to provide shade during the central hours of the day. The enclosures also included one or two females (and in some cases one small male; see table 1). All females were randomly assigned to enclosures and/or males, except that females' SVL had to be at least 5 mm less than the males' (in the field, males were associated with smaller females).

I placed a blind 7.5 m away from the enclosure. Using suspended fishing lines, I could move an intruder from behind the blind to inside the enclosure and retrieve it at the end of the trial without my ever leaving the blind. When I approached the enclosures for feeding or small repairs I used a poncho which contrasted with the clothes used during tests (white pants and T-shirt).

The enclosures were more than 15 m apart with dense and tall intervening vegetation ensuring no visual contact between them and were placed in areas where, during a period of ten months, I only observed four free-ranging adults *T. hispidus* (one male and three females). Thus, interactions with naturally occurring conspecifics should have been extremely rare.

The lizards were fed a diet of crickets, mealworms, fly maggots, roaches and beetles and a mixture of egg, powdered milk and fruit every two to three days. In experiment 1, water was available naturally (rainy season) and the animals were fed one or two days before testing started and were not fed during the days of testing. In experiment 2 (dry season), the enclosures had several water containers and the animals were fed one or two days preceding testing and early on the third day or, after testing, on the second day. The enclosures were cleaned of fecal boli before introducing new experimental animals.

The animals in the enclosures displayed normal anti-predator behaviour: *T. hispidus* uses refuges for hiding when a predator attacks (Vitt 1995) and in the study area I observed wild *T. hispidus* run into refuges when attacked by the predators—dogs, cats, chickens and common marmosets (*Callithrix jacchus*)—and when potential predators (e.g. crane hawks (*Geranospiza caerulescens*) and caracaras (*Polyborus plancus*)) flew over. Moreover, in this region of Brazil, *T. hispidus* are very frequently killed by humans (particularly children). The *T. hispidus* in the enclosures not only sought refuge when approached by a human, but also when crane hawks and caracaras flew over.

The animals in the enclosures also displayed normal aggressive and mating behaviour: males attacked intruders and courted and mated with females; more than nine females laid eggs and at least six clutches hatched successfully in the enclosures. Body mass did not change between the time the

Table 1. *Experiments 1 and 2: methods*

sequences <sup>a</sup>	subjects	treatments
experiment 1: EC, CE	<p>three batches of six enclosures each with one experimental male per enclosure</p> <p>each enclosure also two females (four enclosures) or one female and one small male (two enclosures)<sup>b</sup>; females and small males were the same in each enclosure throughout the experiment</p> <p>experimental males assigned randomly to enclosures</p> <p>three males in each batch assigned randomly to each sequence</p> <p>males tested after six to seven days in enclosures</p> <p>sample size: 15 males<sup>c</sup></p>	<p>extended (E):</p> <p>introduced intruder male left in enclosure maximum 15 min once attacked, left for 3 min and until three attacks</p> <p>remove intruder</p> <p>anti-predator test (see text); time end of intruder presentation to anti-predator test: 5 min</p> <p>control (C):</p> <p>introduced wood stick (approximately same colour and size as adult male)</p> <p>left in enclosure for 3 min 45 s<sup>d</sup></p> <p>remove control</p> <p>anti-predator test; time end of control presentation to anti-predator test: 5 min</p>
experiment 2: EIII, IEEI	<p>six different enclosures used repeatedly, no batches</p> <p>one female and one experimental male introduced simultaneously in each enclosure (i.e. different females for each male)</p> <p>males assigned randomly to enclosures</p> <p>first animal tested assigned sequence at random; successive animals assigned immediately (before testing) alternating sequences</p> <p>males tested when habituated (after 5 to 12 days in enclosures)</p> <p>sample size: 12 males<sup>c</sup></p>	<p>extended (E):</p> <p>introduced intruder male left in enclosure maximum 15 min once attacked, left for 2 min (and a minimum of four attacks) or until six attacks, whichever came first</p> <p>remove intruder</p> <p>anti-predator test; time end of intruder presentation to anti-predator test: 5 min</p> <p>immediate (I):</p> <p>introduced intruder male left in enclosure maximum 15 min once attacked, left for 2 min (and a minimum of four attacks) or until six attacks, whichever came first</p> <p>anti-predator test; i.e. intruder still within enclosure</p> <p>intruder removed immediately after lizard hid</p>

<sup>a</sup> A sequence is the order in which the within-individual treatments are applied. An animal is assigned to a sequence, and treatments applied in the specified order (e.g. for sequences EC in experiment 1, first testing day is E, second testing day is C). Therefore, experiment 1 consisted of two periods and experiment 2 of four periods, where a period is each one of the testing days.

<sup>b</sup> In the field, a male's territory overlaps the territory of one or more females and often the home range of one or more small males.

I never observed aggressive interactions between the experimental male and the small male.

<sup>c</sup> One of the enclosures could only be used during the first week and one animal was excluded from the study (it was hiding continuously during the day of testing).

<sup>d</sup> Median time that an intruder spent in the enclosure in preliminary trials.

<sup>e</sup> I obtained data for all four periods for all animals except two, one from each of the sequences.

<sup>f</sup> In the I-treatment, removing the intruder from the enclosure took 1 min and involved some movement of the intruder delivery system. To control for these effects, in the E-treatment after the animal hid I approached the enclosure and remained next to it for 1 min, while moving the intruder delivery system to mimic the effects of removing an intruder.

animals were introduced and the time they were removed from the enclosures (experiment 1 mean change (final–initial mass)  $\pm$  s.e. =  $-0.27 \pm 0.409$  g, paired  $t_{14} = 0.67$  and  $p = 0.512$ , and experiment 2 mean change  $\pm$  s.e. =  $1.33 \pm 0.736$  g, paired  $t_{11} = 1.89$  and  $p = 0.085$ ). While in the enclosures, the lizards were rarely approached by humans (except myself).

### (c) *Experimental design and anti-predator tests*

The animals were tested several days (table 1) after being introduced to an enclosure in both experiments to ensure that the animals were used to the enclosures. I used crossover designs (Jones & Kenward 1989): each animal was subjected to two treatments over time, so that the treatment differences were

Table 2. *Response variables used to measure anti-predator behaviour*

(The predictions tested refer to increases in predation risk which result from behavioural changes of the prey. As I could not measure predation risk directly I used the four response variables as proxies (and assumed that the risk of being killed is a decreasing function of each of the response variables). The approach and minimum distances are proxies for the risk when a predator attacks; the time to re-emerge and time to full exposure are proxies for the risk at re-emergence. Thus, the four variables belong to two groups: initial attack and re-emergence. The results within each pair of variables should be consistent (i.e. either none of the two variables will depart from the null hypothesis or the two variables will depart from it in the same direction).)

variable	description
approach distance	distance between observer and the lizard when the lizard first initiated flight
minimum distance	minimum distance between the observer and the lizard before it initiated flight; the same as approach distance if there is only one run
time to re-emerge	time since the lizard hid until it re-emerged (i.e. until at least all the head was visible out of the refuge)
time to full exposure	time since the lizard hid until it was fully exposed (all the lateral surface of the body—not including the tail—was visible out the refuge); lizards in full exposure were generally more than one body length away from the refuge, they were visible (from many sight points) to both other lizards and potential predators and were able to monitor their whole territory

estimated using within-animal comparisons. Each animal received only one treatment per day in the sequences shown in table 1 and was tested on successive days and at approximately the same hour on all days. Thus, the testing phase lasted two days for each animal in experiment 1 and four days for each animal in experiment 2. Both experiments involved presenting a male lizard with a stimulus (intruder or control) and, some time later, measuring anti-predator behaviour by simulating a predatory attack. A test (stimulus presentation plus anti-predator test) lasted *ca.* 40 min per animal.

In experiment 1, I measured anti-predator behaviour 5 min after an intruder encounter (E, extended effects) and 5 min after a control (C) presentation. In experiment 2, I measured anti-predator behaviour during an ongoing aggressive interaction with an intruder (I, immediate effects) and 5 min after the end of the interaction (E, extended effects). Details of the experiments are shown in table 1. When escaping predators *T. hispidus* needs to decide when to flee from the predator and, after hiding, when to re-emerge from the refuge; thus, the variables measured were chosen to reflect these two decisions and are explained in table 2. To run the anti-predator test, I positioned myself 13 m away from the enclosure (4.5 m behind the blind) and approached the lizard directly at a moderate speed (experiment 1, mean = 0.42 m s<sup>-1</sup> and s.d. = 0.056 m s<sup>-1</sup>, and experiment 2, mean = 0.46 m s<sup>-1</sup> and s.d. = 0.047 m s<sup>-1</sup>). Whenever the lizard moved I stopped for 15 s and recorded my position and then approached again. The approach and stop continued until the lizard hid, when I moved to a spot at a fixed distance from the enclosure (experiment 1, 2 m, and experiment 2, 4.5 m) and remained motionless for 20 min. I recorded my movements and the lizard's behaviours using an HP-48GX calculator for continuous event recording. All tests were conducted when the lizards were active and the air temperature (shaded bulb at 1.5 m) higher than 26 °C.

The animals were habituated to the movement of the intruder delivery system using a toothpaste container (to prevent habituation to the control) with which I mimicked the movements I would use during the intruder and control presentations. The lizards were subjected to four to ten habituation trials and were considered habituated if they did not hide during two successive habituation trials. In experiment 2, I initially habituated some animals by hanging soda bottles for 24–48 h next to the enclosures (using the intruder delivery system); later, these animals were checked for habituation using the toothpaste container.

#### (d) *Statistical analyses*

In experiment 1, I analysed the approach distance and minimum distance (table 2) with linear mixed-effects models using the parameterization in Jones & Kenward (1989, p. 30), but also including several covariates and random effects. The full model examined was

$$y_{ijklm} = \mu + \lambda_i + \beta X_j + \alpha_k + c_{j|k,\beta} + w_l + s_{ij(l)} + \pi_m + \tau_{n[i,m]} + (\tau\beta)_n X_j + (\tau\alpha)_{kn} + (\alpha\beta)_k X_j + (\tau\alpha\beta)_{kn} X_j + e_{ijklm}, \quad (1)$$

where, in the fixed effects part,  $\mu$  is the intercept,  $\lambda$  is the carry-over (which in this parameterization is equivalent to a sequence effect),  $\beta$  is the coefficient for the enclosure area ( $X$ ),  $\alpha$  is the type of enclosure (two females or one female and one small male),  $\pi$  is the period effect (a period is each one of the occasions on which a treatment is applied, for example the first or second day),  $\tau$  is the direct treatment effect and the terms in parentheses are interactions. In the random effects part,  $c$ ,  $w$  and  $s$  are the random effects of enclosure, week and individual, respectively and the  $e$ s are the within-individual errors. All the random effects are normal and independent of each other. When analysing the approach distance I included my approach speed and the interaction approach speed multiplied by treatment. For the univariate analyses of experiment 2 (all four variables; table 2), I used the linear mixed model

$$y_{ijklm} = \mu + \xi_i + c_j + (\xi c)_{ij} + s_{ijk} + \pi_m + \tau_{n[i,m]} + \lambda_{n[i,m-1]} + e_{ijklm}, \quad (2)$$

where all the terms are the same as in the model for experiment 1 except  $\xi$ , which denotes the sequence (the sequence is the order in which the within-individual treatments are applied). The model fitting proceeded as in experiment 1 except (i) I modelled the variance-covariance matrix of the within-individual errors  $e$  (examining the fit of compound-symmetrical, autoregressive, general (unstructured positive definite) and heteroscedastic error structures), because the data are repeated (more than two) measures of the same individual, and (ii) if the period (as a categorical variable) was left in the model, I attempted to simplify this structure by fitting linear and quadratic terms of the period as a continuous variable. To fit these models I proceeded as explained in Diggle *et al.* (1994), Littell *et al.* (1996) and Bates & Pinheiro (1999).

In experiment 1, for the time to re-emerge and time to full exposure nine and five out of 30 (i.e. about 0.16 and 0.33) of the observations were right-censored, respectively (i.e. 20 min the lizards still had not re-emerged or fully re-emerged) and, thus, required the use of techniques for censored data. I used the (first) approach suggested in Feingold & Gillespie (1996) after log ranking the observations (e.g. Lawless 1982, p. 420). To obtain  $p$ -values I used systematic permutation tests (Edgington 1995). In experiment 2 the time to re-emerge and time to full exposure had only a few right-censored observations (two and seven out of 46, respectively). Although residual plots did not indicate any problem with the models, I also analysed these data with the method of Feingold & Gillespie (1996), similar to experiment 1.

I measured four response variables in both experiments (table 2). To prevent inferential errors from four univariate tests of potentially correlated response variables and to test for overall differences in anti-predator behaviour taking into account the covariation among response variables, I used the multivariate permutation test for crossover designs of Johnson & Mercante (1996). To give equal weights to all variables I scaled them to a mean of zero and variance of one before computing within-subject contrasts. (Simulations (R. Díaz-Uriarte and E. V. Nordheim, unpublished results) have indicated that the type I error rate of the multivariate test with log-ranked censored data is the nominal one.) I obtained the  $p$ -value for this test using systematic data permutation.

The permutation and multivariate tests were performed with code written in SPlus v.3.3 (Statistical Sciences 1995). For experiment 1, the animals were reassigned to sequences within batches only in all permutation tests; for weeks 2 and 3 the permutation was conditional on the pattern of missing data. Mixed models were fitted using the SPlus library nlme (Bates & Pinheiro 1999) and SAS's PROC MIXED (Littell *et al.* 1996). All  $p$ -values are two-sided.

### 3. RESULTS

#### (a) *Experiment 1: extended effects of aggression on anti-predator behaviour*

The multivariate test showed strong overall evidence of differences between the intruder and control presentations ( $p=0.005$ ). This overall difference is the result of the differences between the control and extended conditions in the time to re-emerge and time to full exposure.

There was evidence of period effects for the time to full exposure ( $p=0.0408$ ) (on the second day, lizards re-emerged fully sooner suggesting habituation). More importantly, for both the time to re-emerge and time to full exposure, lizards re-emerged sooner if they had been in an aggressive encounter instead of subjected to a control treatment (figure 1;  $p=0.0025$  and 0.0058 for time to re-emerge and time to full exposure, respectively). Thus, the results for the time to re-emerge and time to full exposure are consistent and in the direction predicted by the first hypothesis. Analyses using mixed-effects models yielded the same qualitative results. None of the analyses for any of the variables showed evidence of carry-over effects ( $p>0.4$ ).

There were no differences between the control and extended treatments for (log of) the minimum distance. For (square root of) the approach distance I found a significant interaction between the treatment and enclosure areas ( $F_{1,13}=12.86$  and  $p=0.0033$ ): the approach

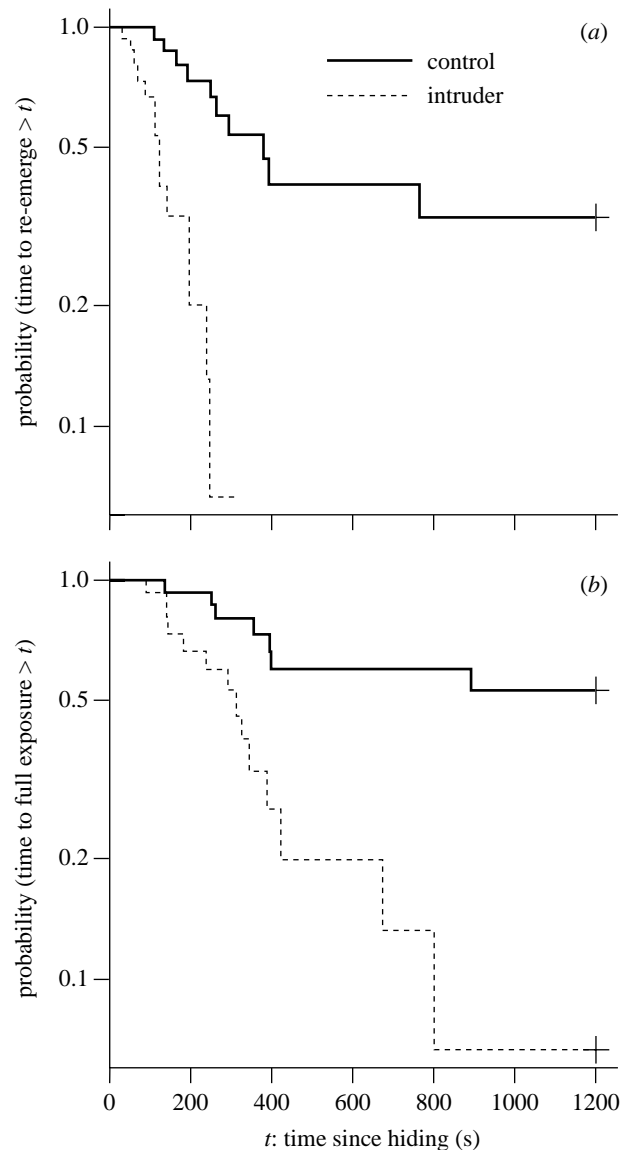


Figure 1. Experiment 1: (a) time to re-emerge and (b) time to full exposure. Survival curves based on the Kaplan–Meier estimator of the survival function. The  $y$ -axis can be interpreted as (a) ‘the probability of not having re-emerged’, and (b) ‘the probability of not having fully re-emerged’. The cross denotes censoring. These figures do not take into account the fact that measures for the same individual are potentially correlated and that there are two distinct sequences; they should not be used directly for hypothesis testing. The  $p$ -values for the treatment effects (analysis following Feingold & Gillespie (1996)) are 0.0025 and 0.0058, respectively.

distance increased with area in the control treatment, but not in the extended treatment (from a reparameterized model, the regression coefficients for the control and intruder presentations are 1.03 and  $-0.385$ , respectively,  $s.e.=0.414$ ;  $t_{18,6}=2.48$  and  $-0.93$  and  $p=0.0227$  and 0.3654). There was weak evidence ( $F_{1,12}=4.51$  and  $p=0.0552$ ) for a main effect of the type of enclosure: the approach distance was larger in enclosures with two females than in enclosures with one female and one small male (back-transformed least-squares means, 7.4 and 4.11 m, respectively). Although the speed of my approach did not differ between treatments (mean difference

intruder–control  $\pm$  s.e. =  $0.018 \pm 0.021$  m s<sup>-1</sup>, paired  $t_{13}$  =  $-0.8675$  and  $p = 0.401$ ), I included my approach speed in the models for the approach distance; neither the main effect nor its interaction with treatment were significant ( $p > 0.3$ ).

**(b) Experiment 2: differences between the extended and immediate effects**

The multivariate test showed strong evidence of the overall differences between the extended and immediate effects ( $p = 0.0130$ ). This overall difference was due to differences in the approach and minimum distances.

The time to re-emerge and time to full exposure did not differ between the extended and immediate treatments. For (log of) the time to full exposure the animals re-emerged sooner in later periods of testing; the final model included only a linear effect of period ( $F_{1,33.2} = 12.41$  and  $p = 0.0013$ ; regression coefficient  $\pm$  s.e. =  $-0.254 \pm 0.072$ ) suggesting habituation. The analyses with Feingold & Gillespie's (1996) method also indicated no treatment effects.

The approach and minimum distances differed between the extended and immediate treatments. For (log of) the minimum distance there were effects of both treatment and period; the final model included a quadratic term for the period ( $F_{1,20.9} = 6.42$  and  $p = 0.0194$ ; coefficient for the linear term =  $0.401$  and coefficient for the quadratic term =  $-0.123$ ), and a term for the treatment ( $F_{1,4.81} = 10.68$  and  $p = 0.0236$ ). As the period of testing progressed, the minimum distance decreased suggesting habituation; more importantly, the minimum distance in the immediate treatment was shorter than in the extended treatment (figure 2). For the approach distance there was only an effect of treatment ( $F_{1,30.2} = 5.65$  and  $p = 0.0240$ ). There was a 7% difference in my approach speed between treatments (the mean speeds for the extended and immediate treatments were  $0.442$  and  $0.473$  m s<sup>-1</sup>, respectively;  $F_{1,29.5} = 5.82$  and  $p = 0.0223$  from a mixed model using lizard as a random effect). However, neither the interaction of the approach speed with treatment nor the main effect of the approach speed had any significant effect on the approach distance (interaction  $F_{1,17.6} = 1.04$  and  $p = 0.3216$  and main effect  $F_{1,8.42} = 0.7$  and  $p = 0.6143$ ). In summary, the results for both the minimum and approach distances are consistent and in the direction predicted by the second hypothesis: the lizards allowed the potential predator to approach closer when they were engaged in an ongoing fight with a conspecific intruder (figure 2).

A possible explanation for the differences in the approach and minimum distances is dilution effects (see §4). In experiment 2, I also recorded whether the female was out of the refuge. If dilution effects are important, experimental lizards should show shorter approach or minimum distances when the female was out of the refuge. I compared the effect of a female out of the refuge on the approach and minimum distances for the extended treatment. I also reanalysed the final models for the approach and minimum distances allowing for the effect of female presence–absence to differ between treatments. In no case was the presence of the female significant (all  $p > 0.15$ ).

Neither experiment compared the immediate effects with a control. However, if we assume that the animals

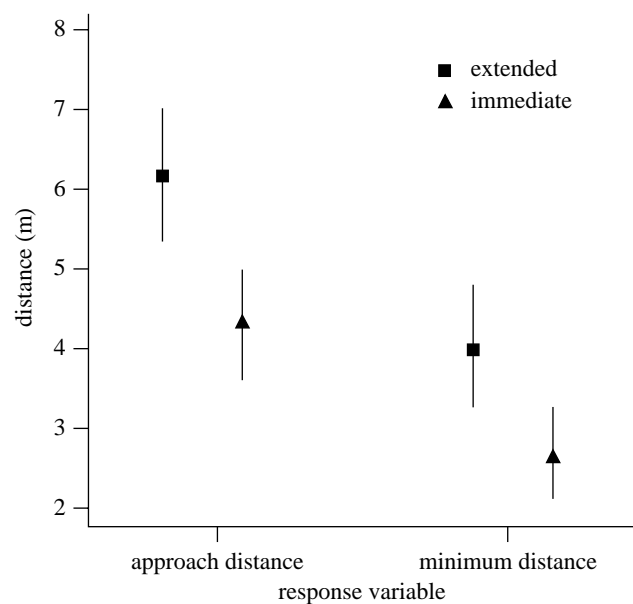


Figure 2. Experiment 2: the approach and minimum distances. Back-transformed adjusted means  $\pm$  s.e. This figure should not be used for hypothesis testing. The  $p$ -values for the treatment effects (from the mixed model) are 0.0240 and 0.0236 for the approach and minimum distances, respectively.

from experiment 2 would have shown differences between the extended and control treatments in the same direction as the animals from experiment 1 did, we can summarize the results from both experiments together as shown in figure 3.

#### 4. DISCUSSION

Past aggressive interactions (experiment 1) decreased the amount of time male *T. hispidus* spent hiding after a simulated predatory attack; when the predator attacked during an ongoing aggressive encounter (experiment 2), the lizards also allowed the predator to approach closer (figure 3). These results show (i) the existence of extended effects of aggressive behaviour on anti-predator behaviour, and (ii) that the extended effects differ from the immediate ones. The results are consistent with the two economic (adaptive) hypotheses stated in §1.

- (i) The past presence of an intruder can indicate an increase in the probability of future intrusions and, therefore, if a predator attacks soon after an aggressive interaction is over a territorial resident should modify its behaviour to decrease the chances of territorial intrusions at the cost of increased predation risks.
- (ii) The current presence of an intruder increases the territorial costs of hiding with respect to the past presence of an intruder and, thus, territorial residents should show further increases in their exposure to predation when the predator approaches during an aggressive encounter.

Extended effects of aggression on anti-predator behaviour (experiment 1) have not been reported before, but the increase in predation exposure when the lizards were involved in a fight 5 min before the attack of the predator

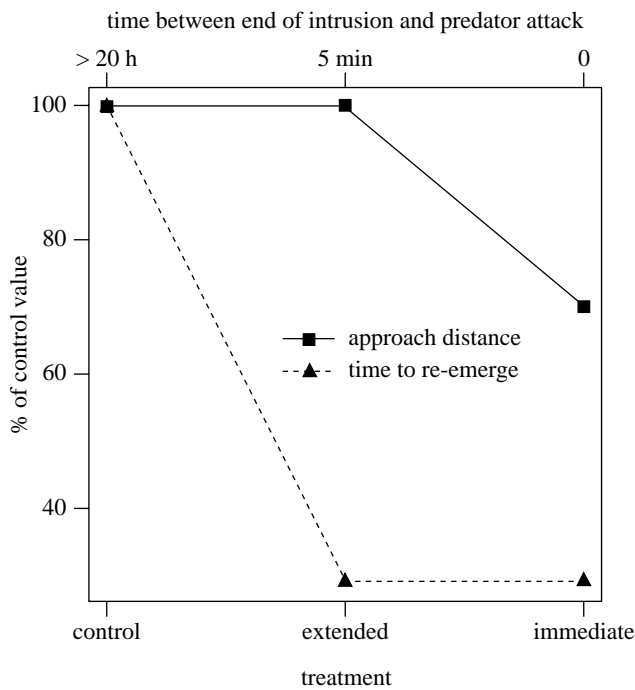


Figure 3. Summary of the results from both experiments based on the approach distance and time to re-emerge. I calculated the 'percentage of the control value' as  $100 \times$  adjusted mean for experimental condition/adjusted mean for control.

is consistent with economic models of anti-predator behaviour (Ydenberg & Dill 1986; Clark 1994). The results indicate that the extended effects mainly affect the re-emergence time, not approach distances. A predatory attack is generally a fast event and the rate of increase in the ability to monitor the territory by delaying flight is probably small compared to the rate of increase in mortality risk. Thus, extended effects on approach distances are likely to be non-existent or difficult to detect when present. In contrast, changes in re-emergence can result in an increased ability to monitor the territory without large increases in mortality risk.

The immediate effects (experiment 2) are consistent with those observed by Jakobsson *et al.* (1995) in both the cichlid *Nannacara anomala* and the warbler *Phylloscopus trochilus*, where animals engaged in an aggressive interaction allow a predator to approach closer than animals exposed to a control stimulus (see also Brick 1998). The data presented here also show that the immediate effects resulted in a decrease in the time to re-emerge (with respect to a control). However, the immediate effects did not result in further decreases in the times to re-emerge compared to the extended effects, despite the potentially larger intrusion costs in the immediate condition (see §1).

In general we should expect different components of anti-predator behaviour to be differentially affected by aggressive interactions, as hiding quickly can have very different consequences in terms of mortality from predation and intruder detection than re-emerging late. These results emphasize the need for measuring the components of the anti-predator strategy which best characterize the key behavioural decisions involved in predator avoidance (e.g. Lima & Dill 1990) and intruder detection.

The immediate effects on the approach and minimum distances (experiment 2) could be explained by the non-adaptive 'sensory limitation hypothesis': an animal involved in a fight might be unable to detect a predator as fast as an animal that is not involved in a fight (e.g. Milinski 1984; Bernays & Wcislo 1994). Sensory limitation seems to be the mechanism invoked by Brick (1998) and Jakobsson *et al.* (1995) to explain the decrease in approach distance during intraspecific fights in both warblers and cichlids. In its most extreme form, the sensory limitation hypothesis predicts that an animal will initiate escape as soon as the predator is detected. In contrast, the economic hypothesis emphasizes the decision component (Ydenberg & Dill 1986): the decrease in approach distance in the immediate treatment would be the result of a change in the perceived cost of hiding and not of a decrease in the ability to detect predators. It is not possible to differentiate between the two hypotheses with the approach distance data, as both make similar predictions regarding the approach distance in the first approach of the predator. It is difficult to determine the exact moment when a predator is detected, but the two hypotheses could be differentiated by increasing the costs of hiding: the economic hypothesis would predict increased exposure to predation, whereas the sensory limitation hypothesis would predict no change in anti-predator behaviour. Further work to elucidate whether the changes in approach distance in the immediate condition are due to sensory limitations, an economic decision or a combination of both is warranted.

A third explanation for the reduction in approach distance in the immediate treatment is dilution effects: if the predator can only capture a single prey the chances that the resident is the victim decrease in the immediate treatment because there are two lizards in the area. The tests in experiment 2 (presence versus absence of a female out of the refuge), although not conclusively excluding dilution effects, suggest that the changes in the approach and minimum distances in the immediate treatment were not solely a result of dilution effects.

In contrast, the differences in the time to re-emerge and time to full exposure between the control and extended conditions (experiment 1) cannot be explained by the sensory limitation hypothesis or dilution effects. Thus, the economic hypothesis provides the best explanation for the changes in the time to re-emerge.

Past aggressive interactions with intruders can affect the subsequent behaviour of a territorial holder. Great tits invest more time in territorial vigilance (at the cost of decreased foraging) after encountering intruders (Kacelnick *et al.* 1981; Ydenberg & Krebs 1987). In the lizard *Sceloporus jarrovi* the frequency of most displays peaks shortly after an encounter (Moore 1987; see also Thompson & Moore (1992) for *Urosaurus ornatus*). Following a previous victory there is an increase in the probability of winning subsequent encounters in several taxa (Chase *et al.* 1994; Adamo & Hoy 1995). Functionally, these different phenomena can be a response by the territorial resident to a transient increase in the probability of reintrusion by the same intruder and the extended effects of aggression on anti-predator behaviour are consistent with minimization of the increased risk of territorial intrusion caused by a transient change in the

probability of future intrusions. Thus, a similar functional explanation can underlie different behavioural phenomena where animals change their aggressive and/or anti-predator behaviour as a response to local changes in their social environments (e.g. Oliveira *et al.* 1998).

The extended effects show a connection between anti-predator and aggressive behaviour which should vary with the defensibility of resources and which can influence the (co)evolution of these sets of traits by increasing both the predation-related costs of territorial behaviour and the territorial costs of hiding. The hypothesis underlying the extended effects is testable using both within- and between-species comparisons. Given that an economic reasoning is the basis of the extended effects, it will also be particularly important to understand the relative contributions of perceptual constraints, dilution effects and increased hiding costs in the effects of an ongoing fight on approach distances and, ultimately, measure the fitness consequences of different anti-predator responses following an aggressive encounter.

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