

A quantitative test of the ‘economic’ and ‘optimal’ models of escape behaviour



Patricio A. Lagos^{a,*}, Luis A. Ebensperger^b, Marie E. Herberstein^a

^a Department of Biological Sciences, Macquarie University, North Ryde, Australia

^b Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

ARTICLE INFO

Article history:

Received 13 June 2014

Initial acceptance 14 July 2014

Final acceptance 15 August 2014

Available online 11 October 2014

MS. number: 14-00483

Keywords:

antipredator behaviour

escape behaviour

FID

flight initiation distance

Escape distance

Two theoretical models, the ‘economic’ and the ‘optimal’ model, have been proposed to explain how the fitness of prey changes in relation to flight initiation distance (FID): the distance between predator and prey when the prey initiates escape. Both hypotheses assume that the cost for the prey of remaining foraging (=capture by a predator) influences their decision to escape and this cost should decrease as FID increases. Much qualitative research supports this prediction; however, no quantitative estimate of the cost of escape behaviour exists. Here, we used a seminatural experiment on predator–prey interactions using the black field cricket, *Teleogryllus commodus*, as prey. We quantified the probability of survival of the prey as an ecological proxy of the cost of remaining at the foraging patch, and the FID of crickets at four different starting distances. The shape of the curve for the prey’s cost of remaining foraging for the ‘economic’ model graphically fits the cost of staying in the patch most closely. The shape of the curve of survival of the prey, as proposed by the ‘optimal model’, is also appropriate, but the equation that best represents this curve is quadratic rather than exponential as suggested by the model mentioned.

© 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Antipredator behaviours reduce the probability of prey being attacked (including pursuit; Conover, 2007; Fitzgibbon, 1990; Lima & Dill, 1990) or captured once an attack ensues (Cresswell, 1993, 1994; Lima, 1995; Lima & Dill, 1990). Thus, escape behaviour contributes to the latter category. In the context of escape behaviour, a foraging prey must decide when to escape. This decision-making process has been suggested to be based on the costs for the prey. This is particularly true when a foraging prey detects an approaching predator. In particular, a trade-off exists between the cost of remaining in the foraging patch (i.e. predation risk) and the cost of losing additional opportunity to forage, because in order to minimize the risk of being captured, the prey must give up food items or mating opportunities. To study this cost trade-off, flight initiation distance (henceforth FID, the distance between the prey and the predator when the former decides to escape) has been widely used (reviewed by Stankowich & Blumstein, 2005).

Ydenberg and Dill (1986) proposed the first theoretical model to explain when the prey should escape. This ‘economic’ model, based on the cost of remaining foraging and the cost of leaving the patch too soon, qualitatively states that the optimal FID should occur when the cost of leaving the patch equals the cost of remaining.

Whenever the cost of remaining foraging outweighs the cost of escaping, the prey is predicted to flee, with FID affecting the cost of remaining foraging in a decreasing exponential trajectory. More interestingly, the hypothesis predicts the existence of an optimal FID, where the cost of remaining foraging and the cost of escaping are equal (Fig. 1a). A slightly different theoretical approach addressed prey that remains motionless when it detects an approaching predator. In this alternative context cryptic prey should either flee immediately after the predator is detected or stand its ground if attacked because an early escape would alert the predator to the presence of the prey (especially if the predator is not yet aware of the presence of the prey; Broom & Ruxton, 2005). A further modification to the ‘economic’ model (Blumstein, 2003) hypothesized the existence of thresholds, with a minimum FID (below which prey will always respond), and a maximum FID (beyond which prey will never respond).

Despite its heuristic value, some of the predictions of this ‘economic’ model may be flawed or incomplete. Under the economic model, prey would not have the choice of maximizing its fitness when facing an approaching predator (Cooper & Frederick, 2007). For instance, an animal might accept closer approaches or fight the predator if that increases the survival of its progeny (Glover, Weston, Maguire, Miller, & Christie, 2011; Liker & Székely, 2005) or enhances mating opportunities (Gwynne, 1989; Magnhagen, 1991). Cooper and Frederick (2007) developed a mathematical model to incorporate this possibility under an

* Correspondence: P. A. Lagos, Department of Biological Sciences, Macquarie University, Eastern Rd, E8 building, North Ryde, NSW 2109, Australia.

E-mail address: palagosc@gmail.com (P. A. Lagos).

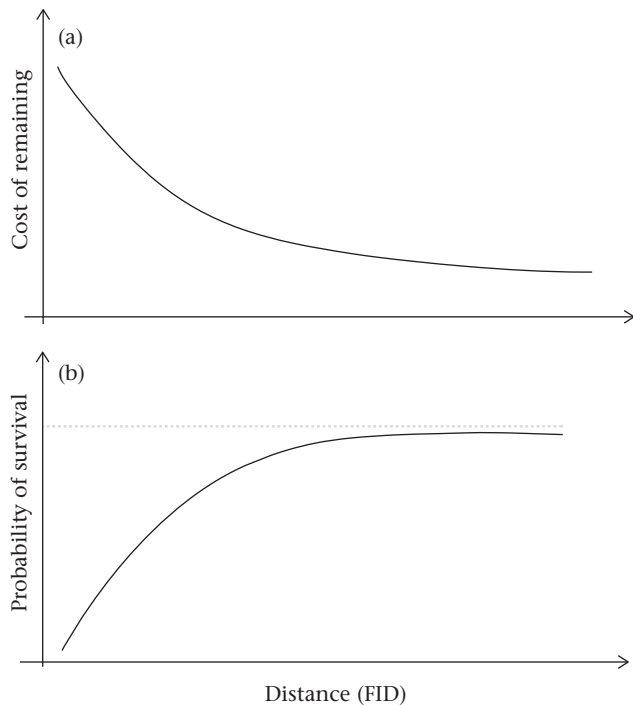


Figure 1. Theoretical curves of (a) the cost of remaining in the patch and (b) the probability of survival for a foraging prey, as proposed by Ydenberg and Dill (1986) and Cooper and Frederick (2007), respectively. As flight initiation distance increases, the probability of survival increases, and the cost of remaining foraging decreases.

optimal, rather than economic, perspective. Predictions of both models are similar, except that under an optimal model, prey may retain some benefits after death. This implies that, under certain circumstances, animals may accept closer approach distances provided that the benefits are large enough, even if the prey is captured (for a comparison of the predictions of the two hypotheses see Table 1 in Cooper & Frederick, 2007). One novel prediction of the optimal model is that the probability of survival of a foraging prey should increase exponentially with FID, with a negative exponent (Fig. 1b).

Ever since the publication of the economic model, studies have examined multiple determinants of FID, including distance to the refuge (Bonenfant & Kramer, 1996; Dill & Houtman, 1987; Lagos et al., 2009), quality of the foraging patch (Cooper et al., 2003; Krause & Godin, 1996; Lagos et al., 2009), size of the foraging group (Beauchamp, 2012; Grovenburg, Monteith, Klaver, & Jenks, 2012; Ydenberg & Dill, 1986), number (Geist, Liao, Libby, & Blumstein, 2005) and speed of predators (Dangles, Casas, & Coolen, 2006; Dangles, Ory, Steinmann, Christides, & Casas, 2006), directness of the attack (Cooper, 2003; Kramer & Bonenfant, 1997) and starting distance of the predator (Blumstein, 2003), among others (see Stankowich & Blumstein, 2005 for a review). To date, all studies conducted have been qualitative in nature, meaning we lack quantitative estimates of prey fitness in a foraging context. Thus, the actual shapes of the cost curves in both economic and optimal models remain theoretical. This represents an important gap in our understanding of anti-predator behaviour, especially if we are to comprehend and predict how animals respond to predators. Importantly, a confirmation of the existing models and their predictions would strengthen the last 25 years of research in this field.

Here, we used an experimental approach on the predator–prey interaction between a reptile predator (lizard) and a foraging insect prey (cricket). We measured FID and the probability of survival for a

foraging prey (as an ecological proxy for fitness) when it faces an approaching predator. We predicted that the probability of survival will increase with FID, as proposed by Cooper and Frederick (2007), because the probability of reaching a safe refuge or outrunning the predator would increase with larger FIDs. We also predicted that the cost of remaining in the foraging patch will decrease with increasing FID according to the economic model due to a lower probability of being captured. To our knowledge, this represents the first successful attempt to experimentally measure the curve of survival probability and the shape of the cost curve of a foraging prey.

METHODS

Study Species

We studied interactions between black field crickets, *Teleogryllus commodus*, as prey and eastern water skinks, *Eulamprus quoyii*, as predators in the laboratory, between July 2012 and February 2013. Four adult female *E. quoyii* were used as predators. These two species coexist in a large area around Sydney, making this predator–prey system particularly suitable for testing our hypotheses, as a pilot experiment showed. For the experiment, only female crickets were used, since different sexes may have different antipredator behaviours (Worthington & Swallow, 2006), and these might include differences in FID.

Ethical Note

Crickets were bred in the laboratory and kept in a plastic box with food (Friskies Senior) and water ad libitum (Kasumovic, Hall, & Brooks, 2012). Those crickets that survived after the experiment were kept separately from the rest of the colony, and were not reused. Whenever possible, trials that did not meet our criteria were stopped before the lizard could capture the cricket, reducing the number of animals used in the experiment.

The skinks were part of an existing captive colony used by other researchers for behavioural experiments. They were kept in outdoors facilities at Macquarie University, where they were housed in round tubs (3 m diameter), in groups of about eight individuals of the same sex. This is similar to densities found in the field, where it is easy to find them every few metres. The tubs were partially covered to provide shade, and clay tiles were provided in excess as refuges, allowing the animals to have their own space. There, they had water ad libitum and were fed three times a week in summer and twice a week in winter, with domestic crickets. Before our experiment was conducted, skinks were moved indoors, using cloth bags (one individual per bag). Indoors facilities consisted of a room, kept at 25 °C and environmental humidity, with 12:12 h light:dark cycles (fluorescent tubes were used as the source of light). Animals were kept in plastic tubs (40 × 30 cm and 30 cm high), one per tub. Having one animal per tub was not considered stressful, since this is not a group-living species, and they have been housed in the same conditions for previous experiments, and always fed and behaved normally. In any case, the health of every animal was constantly assessed by checking that they fed and behaved normally. Under each tub, an electrical warm wire was placed, to keep the temperature of the box as constant as possible. A small black box was provided as a refuge, and the bottom of the tub was covered with paper, which was replaced every week as part of the cleaning process. For the experiment, skinks were moved from their tubs to the experimental arena by gently turning the tub over the arena, minimizing the handling of the animal. The same procedure was performed to return the animal to its tub. When the trials were finished, animals were returned to the outdoor enclosures.

The experiment adhered to the animal ethics regulations of Macquarie University, in accordance with Australian animal welfare standards (Animal Research Authority, number of project: ARA 2012-062).

Experimental Design

To study the effect of FID on the cost of remaining foraging, an arena was prepared, consisting of a plastic box (60 × 40 cm and 40 cm high). The bottom was covered with graph paper, which provided both a rough surface for the animals to move on and also allowed us to measure distances with a precision of 0.5 cm. Additionally, a 30 cm ruler was placed in a corner. The cricket was released at a foraging patch, at varying distance (see below) to the skink predator. To provide the crickets with a refuge, a pack of egg cartons was placed 10 cm from the foraging patch, diametrically opposite the position of the skink. A surveillance camera (AVerMedia AVerDiGi SEB3104H) was placed above the arena, to record each trial.

A single adult female cricket was introduced into the arena, inside an upside down plastic jar (6 cm diameter × 8 cm height). At the same time, one skink was introduced into the arena, inside a small, black plastic box (17 × 12 cm and 6 cm high). By doing this, we could manipulate the distance between the lizard and the cricket (i.e. starting distance) before the trial started. A thread was attached to the top of the jar, to pull it up without disturbing the cricket (Fig. 2).

The side of the jar facing the skink was covered with duct tape to prevent the cricket from visually detecting the predator, but the other half of the jar was not covered, so the cricket could still see the refuge.

We provided a single piece of dry cat food (Friskies Senior, 0.16 ± 0.018 g, $N = 79$) to the cricket in the jar, thus controlling for any effect of the quality of the patch, a factor known to influence FID (Stankowich & Blumstein, 2005). We also did not feed crickets for 2 days prior to the trial to ensure they would need to forage, but they did have constant access to water (Booman, Folkvord, & Hunter, 1991).

The trial began when the cricket started feeding at the patch. At that point, the skink and cricket were released by simultaneously lifting the jar and the box that enclosed them. We filmed the entire skink–cricket interaction and noted whether the cricket survived the attack or not. We recorded the following parameters: starting distance (distance between cricket and lizard), latency to attack (measured as the time between the release of the cricket and the start of the attack), FID, survival of the cricket and the identity of the skink used.

In some cases (ca. 5% of all trials) crickets did not escape directly into the refuge, and the skink had the chance to attack a second time. These instances were not considered during further analyses since the risk associated with the second attack is different (and not comparable) to the risk at the start of the encounter. To standardize attack trajectory, we only considered trials in which the skink attacked the cricket directly in a straight line from its starting position. Skinks that did not attack or attacked indirectly and cases where the skink moved outside the visual range of the cricket (defined a priori as 180° in front of the cricket) were not included in the analyses. Of 200 trials, 79 (39.5%) met our criteria as valid trials.

Four starting distances were chosen a priori (1, 5, 10 and 15 cm), and the four skinks used were randomized between these four starting distances. Initially, we also trialled a starting distance of 20 cm, but it was not always evident that the cricket was able to detect the skink at this distance, so it was excluded from the experiment. Because there is no agreement on whether starting distance (Blumstein, 2003; Cooper, Hawlena, & Pérez-Mellado, 2009; Geist et al., 2005; Runyan & Blumstein, 2004; Stankowich & Coss, 2006, 2007) or alert distance (Blackwell, Fernández-Juricic, Seamans, & Dolan, 2009; Blumstein, Fernández-Juricic, Zollner, & Garity, 2005; Cárdenas, Shen, Zung, & Blumstein, 2005; Fernández-Juricic, Jimenez, & Lucas, 2002; Fernández-Juricic, & Schroeder, 2003) should be used in this kind of experiment, we selected the four starting distances in a way that the prey would detect the predator at the same moment the trial started (i.e. starting distance = alert distance), as has recently been proposed (Dumont, Pasquaretta, Réale, Bogliani, & Von Hardenberg, 2012). Hereafter, we refer to it as starting distance.

Statistical Analyses

The outcome of every trial was tallied as either 'cricket captured' or 'cricket survived', two mutually exclusive categories. Accordingly, we used logistic regression to analyse the probability of cricket survival, with survival of the cricket as the dependent variable. FID and latency to attack were used as continuous predictors, and starting distance (four levels: 1, 5, 10 and 15 cm) and skink ID (four levels: skink 1, 2, 3 and 4) were used as categorical predictors. We analysed the effects of starting distance, latency to attack, skink ID and FID on the probability of survival of crickets, using logistic regression. We also evaluated the effect of starting distance, latency to attack and skink ID on FID using a generalized linear model. To select the most parsimonious models (i.e. the model that explained most of the variability in the dependent variables using the fewest independent variables), we used Akaike's information criterion.

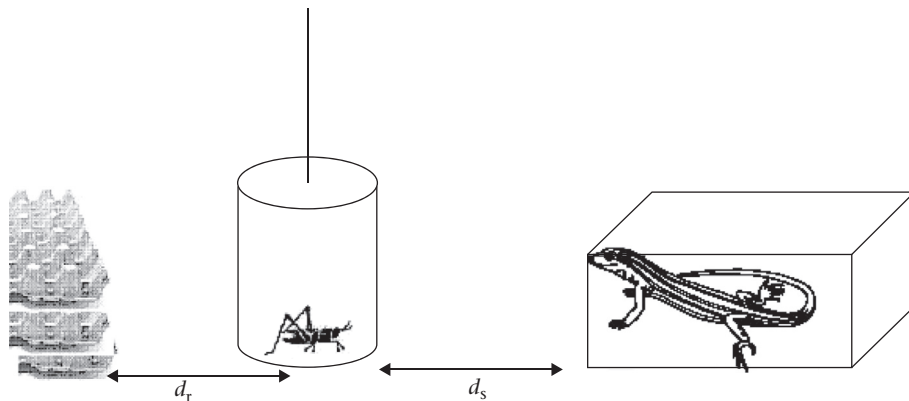


Figure 2. Experimental set-up. From left to right: pack of egg cartons (refuge for the cricket); jar containing the food and the cricket; skink inside a black box (not coloured here for purposes of the diagram). d_r is the distance to the refuge (constant in all the experiments) and d_s is the starting distance (1, 5, 10 or 15 cm).

To identify the shape of the curve of survival of crickets, we compared four different models (exponential, quadratic, logistic and cubic), using equations that may resemble the theoretical shape proposed by Cooper and Frederick (2007). To determine which was the best fit to our data, log-likelihood analysis was used. The exponential and quadratic equations were selected because they graphically resemble the theoretical curve of survival proposed by Cooper and Frederick (2007). We also included the hyperbolic function, but the log-likelihood score was too low compared to the other equations, and was not included in the results. Likewise, the cubic and logistic equations were used to test the existence of thresholds, as proposed by Blumstein (2003).

All analyses were run on R version 3.0.1 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>). Results are expressed as mean $\pm$ SD. Unless otherwise specified, the number of trials was 79.

RESULTS

Crickets showed a very distinctive antipredator behaviour. When they detected the skink, they stopped foraging and remained motionless, occasionally moving only their antennae. Even when the skinks started approaching, crickets did not escape immediately. On average, crickets escaped when predators were within 1.44 ± 1.72 cm ($N = 79$) resulting in a probability of survival of 0.582 ± 0.496 . FID was the only factor significantly affecting the probability of survival: crickets escaping at longer FIDs showed a higher probability of survival (logistic regression: $P = 0.0002$, $r^2 = 0.333$, effect size $r = 0.577$).

Starting distance did not significantly affect the probability of survival (logistic regression: $P = 0.707$, $r^2 = 0.009$). In contrast, there was a slight yet significant effect of starting distance on FID (generalized linear model: $P = 0.013$, $r^2 = 0.065$, effect size $r = 0.255$; Fig. 3). Moreover, starting distance did not significantly affect the latency to attack (generalized linear model: $P = 0.282$, $r^2 = 0.002$).

Latency to attack was highly variable (71.03 ± 101.80 s) and did not affect the probability of survival (logistic regression: $P = 0.343$, $r^2 = 0.0002$) or FID (generalized linear model: $P = 0.403$, $r^2 = 0.004$). However, latency to attack varied with skink ID (generalized linear model: $P = 0.045$, $r^2 = 0.038$, effect size $r = 0.195$), but not with starting distance (see above).

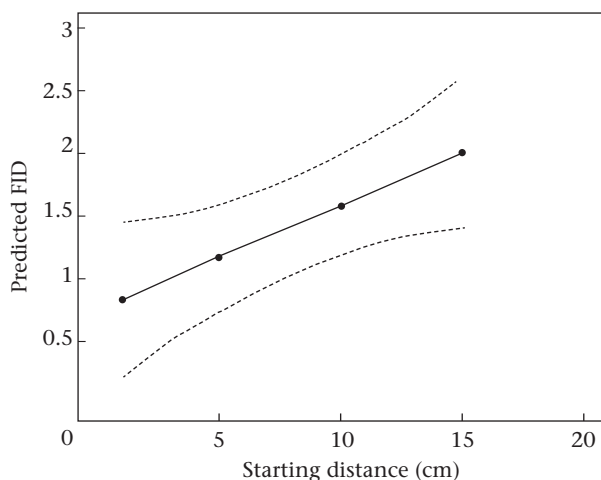


Figure 3. Flight initiation distance of crickets as a function of starting distance (i.e. the distance between the cricket and the predator at the beginning of the trial), as predicted by our empirical data. Dashed lines indicate 95% interval of confidence.

Table 1
Competing models explaining the probability of survival for crickets

Model	Coefficient	P	Log-likelihood
Exponential ^a	1.109	3.3e-08	−33.55
Logistic	B0 = −0.901; B1 = 1.183	0.012; 0.0002	−40.38
Quadratic	1.051	0.0002	−29.66
Cubic	1.715	2.9e-05	−30.47

^a Cooper and Frederick (2007).

Log-likelihood analysis was used to determine the curve that best fitted our data. Of the four equations compared (Table 1), the quadratic one provided the best fit. Thus, the predicted probability of survival was related to FID in a quadratic fashion, with a negative exponent, and asymptotically approached 1 (Fig. 4a), following the equation: $P_{\text{survival}} = 1 - (1 + A \times \text{FID})^{-2}$. The estimated value for the parameter $A = 1.051$ (Table 1).

One data point in Fig. 4a appeared to be an outlier, with an FID of 13 cm (not shown in the figure). We decided to keep this value in the analyses for two reasons. First, it was the actual behaviour of the cricket, and that cricket received the same treatments as all other crickets. Second, this data point helps to illustrate what happens at an FID larger than the average. As Fig. 4a shows, the probability of survival is close to one when FID is large.

The cost of remaining foraging could be calculated from the probability of survival, assuming that predation is the primary or only cost associated with remaining foraging. In that case, $P_{\text{survival}} + P_{\text{capture}} = 1$. Therefore, $1 - P_{\text{survival}} = P_{\text{dying}}$ describes the probability of dying, and its expression would be $P_{\text{dying}} = (1 + A \times \text{FID})^{-2}$. Using this relationship we generated Fig. 4b in which the cost of remaining in the patch decreases exponentially with FID, approaching zero quickly.

DISCUSSION

For many years, behavioural ecologists have been examining different factors affecting escape behaviour (Stankowich & Blumstein, 2005) based on predictions from Ydenberg and Dill's

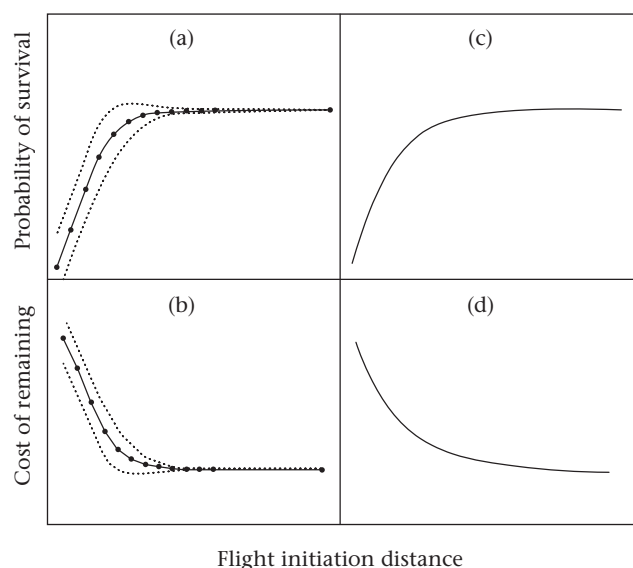


Figure 4. Graphical comparison between (a) the experimental curves of the probability of survival recorded during this study, (b) the empirical curve of the cost of remaining foraging, (c) theoretical curve of probability of survival according to Cooper and Frederick (2007) and (d) the theoretical cost of remaining foraging according to Ydenberg and Dill (1986). Dashed lines represent 95% confidence interval.

(1986) model. These studies have provided abundant qualitative support, yet the predicted curves of costs remained theoretical. The results from our experiment provide the first empirical measurement of the actual probability of survival for a foraging prey under predation risk using different FIDs as predictor. Our results showed that FID accounts for approximately 33% of the variability in the probability of survival. This figure represents a relatively large amount of variation given that FID was the only predictor examined. Other factors linked to the predator such as speed of the predator or predator efficacy and accuracy during prey capture and subjugation may have contributed to the yet unmeasured variation. Similarly, features and traits of the cricket prey, such as age, agility or personality may have had an effect on the probability of survival.

Most of the literature on escape behaviour has focused on vertebrates (see Stankowich & Blumstein, 2005 for a review), which makes studies on predation risk difficult, mainly for ethical reasons. Regarding the few studies conducted on insects, crickets of a different species (*Nemobius sylvestris*) escape at 1.6 cm from a wolf spider (*Pardosa* spp.) predator (Dangles, Casas, & Coolen, 2006; Dangles, Ory, et al., 2006), similar to our findings (1.4 cm). Notably, studies with other species of orthopterans found larger FIDs. The grasshopper *Dissosteira carolina*, for example, had an FID of 1.7 ± 0.2 m when approached slowly, and 3.3 ± 0.3 m when the predator approached at faster speeds (Cooper, 2006). Similarly, the grasshoppers *Psinidia fenestralis* and *Schistocerca alutacea* showed FIDs of 0.9 ± 0.4 m and 2.3 ± 1.3 m, respectively (Bateman & Fleming, 2014). FID generally increases with the size of prey, a finding reported in fishes (Januchowski-Hartley, Nash, & Lawton, 2012), birds (Blumstein, 2003; Eason, Sherman, Rankin, & Coleman, 2006; Geist et al., 2005; Weston, McLeod, Blumstein, & Guay, 2012), lizards (Cooper, 2005; Cooper & Sherbrooke, 2013) and small mammals (Bonenfant & Kramer, 1996; Dill & Houtman, 1987; Lagos et al., 2009). The positive relationship between body size and FID has been demonstrated in birds (Blumstein, 2006), but this pattern seems not to hold in amphibians, which can have FIDs of only a few centimetres (Martín, Luque-Larena, & López, 2005; Tidwell & Hayes, 2013).

Crickets in our study behaved as predicted for a cryptic animal, and allowed us to evaluate the predictions of the 'economic' and 'optimal' theoretical models. Broom and Ruxton (2005) predicted that animals relying heavily on crypsis should either flee as soon as they detect the predator or flee when being attacked. Our experiment showed that crickets refrain from escape until the very last moment, which supports predictions from this model. These authors further suggested that this response of cryptic prey should not be affected by whether the predator attacks the prey immediately or delays the attack. The observation that the latency to skink attack did not affect escape behaviour of crickets confirmed this expectation (but see Cooper, López, Martín, & Pérez-Mellado, 2012; Martín, Luque-Larena, & López, 2009).

Our results provide the first empirical and quantitative estimation of the cost of remaining foraging when a potential prey is approached by a predator. In fact, the empirical curves estimated (Fig. 4a, b) showed remarkable resemblance to the curves of theoretical models ('optimal' model, Fig. 4c, and 'economic' model, Fig. 4d). Our statistical analysis suggested that the exponential optimal model (Cooper & Frederick, 2007) offers a good fit for the shape of the curve of prey survival, but a more thorough analysis of our data showed that a quadratic model represents an even better fit. In fact, based on the log-likelihood scores, the quadratic model is approximately four times more likely than an exponential model. Graphically, both models are similar, but the quadratic model is a better fit for quantitative predictions on the effect of FID in relation to the prey's cost of remaining foraging. Regarding the biological

meaning of the equation that best fitted our data, it is difficult to tell the difference between an exponential and quadratic model on such a small scale. It is possible to think that a system that responds in the way the crickets do will show an exponential curve, not a quadratic one. One possible explanation for a quadratic curve is that some delays exist in the crickets, such as a delay in the neurological response or in the detection of the predator. In this case, the overall response to a predator would be delayed, and the curve of survival may look more quadratic than exponential. Of course, it is also possible that we found a quadratic fit only because our sample size was not large enough.

We found no support for FID thresholds, as proposed by Blumstein (2003). In particular, we found no clear evidence of a minimum FID in the curve showing the cost of remaining foraging. It is still possible that this threshold exists, but because of limitations to the experimental set-up, we were not able to detect it. For example, our experimental design allowed us to measure FIDs with an accuracy of 0.5 cm (ca. one-quarter of the length of an adult cricket), setting a lower limit to the FID that we were able to measure. Thus, the lack of a minimum threshold in our results may be an issue of scale: the threshold may exist, but is too small to be detected with our design. However, such a small threshold would be of little biological relevance: avoiding a predator at such a short distance would be virtually impossible, in particular when facing rapid predators such as skinks. Our results suggest that the cost of remaining foraging keeps increasing when FID decreases, until it reaches the maximum cost possible. Therefore, all the benefits of remaining foraging are reduced to the minimum, not necessarily zero, since being captured may still increase the fitness of the prey under certain circumstances (such as an animal protecting its offspring).

An important parameter linked to the success of the prey's antipredator strategy is the coefficient of curvature, A (c in the 'optimal model'). The smaller the value, the lower the survival, and the flatter the curve. In contrast, large values of parameter A imply steeper curves and high survival rates at short FIDs. For a given FID, animals showing relatively large values of A will have a similarly high probability of survival. This coefficient further informs on the antipredator strategy of the animal. For crickets, a small and cryptic prey that delays escape, the coefficient shows a relatively high value. In comparison, larger, less cryptic (or not cryptic at all) prey that escape at greater distances should exhibit small values of A and a flatter curve of survival. Alternatively, the value of A might be relatively constant across species because prey animals adjust FID exclusively. Clearly, more research is needed to elucidate this aspect of escape behaviour.

Even though starting distance affected FID, and FID affected the probability of survival, starting distance did not directly affect the probability of survival of crickets. This finding suggests that prey can assess the risk that the predator represents at a certain distance, and can change their escape behaviour accordingly (i.e. they can decide when to escape), but cannot modify the starting distance of the predator, a condition set mostly by the predator. Instead, prey may have some control over detection distance (Blumstein, 2003; Blumstein et al., 2005; Lagos et al., 2009) through different mechanisms, including vigilance or the use of open (unobstructed) patches during foraging, both of which may favour an earlier detection of an approaching predator and an earlier escape (i.e. larger FID). Our results agree with the fact that FID is affected by starting (or detection) distance as previously shown in birds (Blumstein, 2003; Blumstein et al., 2005; Eason et al., 2006; Weston et al., 2012), reptiles (Cooper, 2005; Cooper et al., 2009; Cooper & Sherbrooke, 2013) and mammals (Dumont et al., 2012; Lagos et al., 2009; Stankowich & Coss, 2006).

Although we have quantified the cost of remaining foraging we still do not know the actual cost of escaping a patch in terms of lost foraging opportunities. This is an important, yet unquantified component of the economic model and the focus of our current research. Quantifying the actual shape (and equations) of both cost curves would allow us to build more precise models, based on empirical (in addition to theoretical) data. This will give us the ability to make accurate and quantitative predictions about the escape behaviour of animals.

We have examined the escape behaviour of one species of cricket in a very specific ecological context. However, natural settings may be much more complex. Animals live in challenging environments, with different kinds of predators that may have different hunting tactics, as well as nonpredator (anthropogenic) disturbances (Schlacher, Weston, Lynn, & Connolly, 2013). Accordingly, prey may show different antipredator tactics to deal with this variety of threats. For instance, prey that survive an attack are likely to learn from their experience and alter their escape response during future encounters with predators, as a recent study on grasshoppers revealed (Bateman & Fleming, 2014). Modelling these different sources of risk and alternative prey strategies remains challenging, but will take us one step closer to a more comprehensive theoretical framework for understanding the antipredator behaviour of animals.

Acknowledgments

We thank Michael Kasumovic, who gave us the crickets, and Martin Whiting, who provided the skinks for the experiment and helpful comments on the manuscript. P. L. thanks all the students of the lizard's lab at Macquarie University for their help when preparing the manuscript, and CONICYT and Becas Chile for the scholarship to conduct his Ph.D. studies. We thank Macquarie University for providing the funding to conduct the experiment.

References

- Bateman, P. W., & Fleming, P. A. (2014). Switching to plan B: changes in the escape tactics of two grasshopper species (Acrididae: Orthoptera) in response to repeated predatory approaches. *Behavioral Ecology and Sociobiology*, 68, 457–465.
- Beauchamp, G. (2012). Flock size and density influence speed of escape waves in semipalmated sandpipers. *Animal Behaviour*, 83, 1125–1129.
- Blackwell, B., Fernández-Juricic, E., Seamans, T., & Dolan, T. (2009). Avian visual system configuration and behavioural response to object approach. *Animal Behaviour*, 77, 673–684.
- Blumstein, D. T. (2003). Flight-initiation distance in birds is dependent on intruder starting distance. *The Journal of Wildlife Management*, 67(4), 852–857.
- Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*, 71, 389–399.
- Blumstein, D. T., Fernández-Juricic, E., Zollner, P. A., & Garity, S. C. (2005). Inter-specific variation in avian responses to human disturbances. *Journal of Applied Ecology*, 42, 943–953.
- Bonenfant, M., & Kramer, D. L. (1996). The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. *Behavioral Ecology*, 7(3), 299–303.
- Booman, C., Folkvord, A., & Hunter, J. R. (1991). Responsiveness of starved northern Anchovy *Engraulis mordax* Larvae to predatory attacks by adult Anchovy. *Fishery Bulletin*, 89(4), 707–711.
- Broom, M., & Ruxton, G. D. (2005). You can run- or you can hide: optimal strategies for cryptic prey against pursuit predators. *Behavioral Ecology*, 16, 534–540.
- Cárdenas, Y. L., Shen, B., Zung, L., & Blumstein, D. T. (2005). Evaluating temporal and spatial margins of safety in galahs. *Animal Behaviour*, 70, 1395–1399.
- Conover, M. R. (2007). *Predator-prey dynamics: The role of olfaction*. Boca Raton, FL: CRC Press.
- Cooper, W. E. (2003). Effect of risk on aspects of escape behavior by a lizard, *Holbrookia propinqua*, in relation to optimal escape theory. *Ethology*, 109, 617–626.
- Cooper, W. E. (2005). When and how do predator starting distances affect flight initiation distance? *Canadian Journal of Zoology*, 83, 1045–1050.
- Cooper, W. E. (2006). Risk factors and escape strategy in the grasshopper *Dissosteira carolina*. *Behaviour*, 143, 1201–1218.
- Cooper, W. E., & Frederick, W. G. (2007). Optimal flight initiation distance. *Journal of Theoretical Biology*, 244, 59–67.
- Cooper, W. E., Hawlena, D., & Pérez-Mellado, V. (2009). Interactive effect of starting distance and approach speed on escape behavior challenges theory. *Behavioral Ecology*, 20, 542–546.
- Cooper, W. E., López, P., Martin, J., & Pérez-Mellado, V. (2012). Latency to flee from an immobile predator: effects of predation risk and cost of immobility for a prey. *Behavioral Ecology*, 23(4), 790–797.
- Cooper, W. E., Pérez-Mellado, V., Baird, T., Baird, T. A., Caldwell, J. P., & Vitt, L. J. (2003). Effects of risk, cost, and their interaction on optimal escape by non-refuging Bonaire whiptail lizards, *Cnemidophorus murinus*. *Behavioral Ecology*, 14, 288–293.
- Cooper, W. E., & Sherbrooke, W. C. (2013). Effects of recent movement, starting distance and other risk factors on escape behaviour by two phrynosomatid lizards. *Behaviour*, 150, 447–469.
- Cresswell, W. (1993). Escape responses by redshanks, *Tringa totanus*, on attack by avian predators. *Animal Behaviour*, 46, 609–611.
- Cresswell, W. (1994). Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Animal Behaviour*, 47, 433–442.
- Dangles, O., Casas, J., & Coolen, I. (2006). Textbook cricket goes to the field: the ecological scene of the neuroethological play. *Journal of Experimental Biology*, 209(3), 393–398.
- Dangles, O., Ory, N., Steinmann, J. P., Christides, P., & Casas, J. (2006). Spider's attack versus cricket's escape: velocity modes determine success. *Animal Behaviour*, 72, 603–610.
- Dill, L. M., & Houtman, R. (1987). The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). *Canadian Journal of Zoology*, 67, 233–235.
- Dumont, F., Pasquaretta, C., Réale, D., Bogliani, G., & Von Hardenberg, A. (2012). Flight initiation distance and starting distance: biological effect or mathematical artefact? *Ethology*, 118, 1051–1062.
- Eason, P. K., Sherman, P. T., Rankin, O., & Coleman, B. (2006). Factors affecting flight initiation distance in American robins. *Journal of Wildlife Management*, 70(6), 1796–1800.
- Fernández-Juricic, E., Jimenez, M. D., & Lucas, E. (2002). Factors affecting intra- and inter-specific variations in the differences between alert distances and flight initiation distances for birds in forested habitats. *Canadian Journal of Zoology*, 80, 1212–1220.
- Fernández-Juricic, E., & Schroeder, N. (2003). Do variations in scanning behaviour affect tolerance to human disturbance? *Applied Animal Behaviour Science*, 84, 219–234.
- Fitzgibbon, C. D. (1990). Anti-predatory strategies of immature Thompson's gazelles: hiding and the prone response. *Animal Behaviour*, 40, 846–855.
- Geist, C., Liao, J., Libby, S., & Blumstein, D. T. (2005). Does intruder group size and orientation affect flight initiation distance in birds? *Animal Biodiversity and Conservation*, 28(1), 69–73.
- Glover, H. K., Weston, M. A., Maguire, G. S., Miller, K. K., & Christie, B. A. (2011). Towards ecologically meaningful and socially acceptable buffers: response distances of shorebirds in Victoria, Australia, to human disturbance. *Landscape and Urban Planning*, 103(3), 326–334.
- Groenbourg, T. W., Monteith, K. L., Klaver, R. W., & Jenks, J. A. (2012). Predator evasion by white-tailed deer fawns. *Animal Behaviour*, 84, 59–65.
- Gwynne, D. T. (1989). Does copulation increase the risk of predation? *Trends in Ecology & Evolution*, 4(2), 54–56.
- Januchowski-Hartley, F. A., Nash, K. L., & Lawton, R. J. (2012). Influence of spear guns, dive gear and observers on estimating fish flight initiation distance on coral reefs. *Marine Ecology Progress Series*, 469, 113.
- Kasumovic, M. M., Hall, M. D., & Brooks, R. C. (2012). The juvenile social environment introduces variation in the choice and expression of sexually selected traits. *Ecology and Evolution*, 2(5), 1036–1047.
- Kramer, D. L., & Bonenfant, M. (1997). Direction of predator approach and the decision to flee to a refuge. *Animal Behaviour*, 54, 289–295.
- Krause, J., & Godin, J. G. J. (1996). Influence of prey foraging posture on flight behaviour and predation risk: predators take advantage of unwary prey. *Behavioral Ecology*, 7(3), 264–271.
- Lagos, P. A., Meier, A., Ortiz-Tolhuysen, L., Castro, R. A., Bozinovic, F., & Ebensperger, L. A. (2009). Flight initiation distance is differentially sensitive to the costs of staying and leaving food patches in a small-mammal prey. *Canadian Journal of Zoology*, 87, 1016–1023.
- Liker, A., & Székely, T. (2005). Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution*, 59(4), 890–897.
- Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, 49, 11–20.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68, 619–640.
- Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology & Evolution*, 6(6), 183–186.
- Martin, J., Luque-Larena, J. J., & López, P. (2005). Factors affecting escape behavior of Iberian green frogs (*Rana perezi*). *Canadian Journal of Zoology*, 83(9), 1189–1194.
- Martin, J., Luque-Larena, J., & López, P. (2009). When to run from an ambush predator: balancing crypsis benefits with costs of fleeing in lizards. *Animal Behaviour*, 78, 1011–1018.
- Runyan, A. M., & Blumstein, D. T. (2004). Do individual differences influence flight initiation distance? *Journal of Wildlife Management*, 68(4), 1124–1129.

- Schlacher, T. A., Weston, M. A., Lynn, D., & Connolly, R. M. (2013). Setback distances as a conservation tool in wildlife-human interactions: testing their efficacy for birds affected by vehicles on open-coast sandy beaches. *PloS One*, 8(9), e71200.
- Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences*, 272(1581), 2627–2634.
- Stankowich, T., & Coss, R. G. (2006). Effects of predator behaviour and proximity on risk assessment by Columbian black-tailed deer. *Behavioral Ecology*, 17, 246–254.
- Stankowich, T., & Coss, R. G. (2007). Effects of risk assessment, predator behaviour, and habitat on escape behaviour in Columbian black-tailed deer. *Behavioral Ecology*, 18, 358–367.
- Tidwell, K. S., & Hayes, M. P. (2013). Difference in flight initiation distance between recently metamorphosed Oregon Spotted frogs (*Rana pretiosa*) and American bullfrogs (*Lithobates catesbeianus*). *Herpetological Conservation and Biology*, 8(2), 426–434.
- Weston, M. A., McLeod, E. M., Blumstein, D. T., & Guay, P. J. (2012). A review of flight-initiation distance and their application to managing disturbance to Australian birds. *Emu*, 112, 269–286.
- Worthington, A. M., & Swallow, J. G. (2006). Gender differences in survival and antipredatory behaviour in stalk-eyed flies. *Behavioral Ecology*, 21, 759–766.
- Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior*, 16, 229–249.